How Trade Saved Humanity from Biological Exclusion:
An Economic Theory of Neanderthal Extinction [*]

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Abstract: One of the great puzzles in science concerns the rise of early modern humans and the fall of Neanderthals. A number of theories exist and many support the biological principle of competitive exclusion: if two similar species occupy exactly the same niche, only the most efficient will survive; the other will go extinct. Such ideas of biological efficiency pertain to biological or physiological factors. But the evidence for such mechanistic theories in which biology is destiny is limited. In response, this paper develops a behavioral model of Neanderthal extinction. We show how the endogenous division of labor and subsequent trading among early modern humans could have helped them to overcome potential biological deficiencies, and therefore lead to the demise of Neanderthals. We discuss the relation between economics and natural selection, and show how trade may partially offset natural selection.

Keywords: Paleoeconomics, early modern humans, Neanderthals, division of labor, open access, hunting, competitive exclusion

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One of the great scientific puzzles is the cause of Neanderthal (*Homo neanderthalensis)* extinction around 30,000–40,000 B.P., when early modern humans (*Homo sapiens*) started spreading across the world. European Neanderthals are believed to have diverged more than half a million years ago from the lineage giving rise to humans (Mellars 1998), and the first Neanderthal-like creatures appeared around 300,000 B.P. (Gee 1996). Scientists have long asked what explains the species' sudden demise after such a long existence. Many anthropologists and palaeontologists think it was not a coincidence that the fall of Neanderthals occurred at the same time when early humans rose to power. *Homo sapiens* are the suspected culprits, but exactly how early humans triggered Neanderthal extinction remains unsolved.

Notwithstanding the appeal of a unified broad theory to explain the demise of Neanderthals, the literature suggests that multiple causes may have done the species in and that no single theory fits all the available data.1 The core of the current set of theories can be grouped under the principle of competitive exclusion (Mithen 1998; Tattersall and Schwartz 2000; Flores 1998) — the principle that, if two similar species occupy the same niche, only the more efficient survives and the other slowly goes extinct as they compete for resources (see Flores 1998; McGehee and Armstrong 1977). Efficiency in this context can have a mechanistic biological basis or a social or behavioral origin. Prior models have considered a mechanistic biological origin (e.g., Flores)

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[1] Neanderthal extinction was a gradual process involving many distinct and isolated populations (Pettitt 1999). Factors that might explain some local extinctions may not apply to others. The literature provides many ad hoc theories that may or may not be relevant for certain extinctions. Some theories are based on human-Neanderthal interaction through germs and warfare (Diamond 1992) or competition (Flores 1998), and others suggest humans only filled empty niches that arose due to Neanderthal-Neanderthal conflict (Pettitt 1999; Guk 1997). Aggression hypotheses are often discounted since no traces of Paleolithic warfare exist, and because the two species may not have even met in many areas due to low population densities (Pettit 1999). Even if the species did conflict, "this would not have been equivalent to the colonial confrontation between Europeans and Indigenous peoples. There …was no shocking disparity in fire power" (Gamble 1999, p. 268). A hypothesis that the two species "merged" has been ruled out based on DNA evidence that modern humans do not carry Neanderthal genes (Krings et al. 1997).

not rooted in behavior or ethology. By mechanistic, we mean that exogenous forces govern population dynamics because, at the micro level, individuals take these forces to be given and outside of their control. For instance, an individual's meat consumption would be limited by his own skills, physiology, and available technology. Biological efficiency in this context therefore captures the idea that differences existed in exogenous biological factors (as opposed to behavioral factors) like higher birth rates or lower mortality rates, and physiological or technological factors like being better hunters.[2] We refer to competitive exclusion based on biological efficiency thus defined as *biological exclusion*.

Since early man is still around, biological exclusion theories suggest that man must have been more biologically efficient than Neanderthals. This "just-so" story of biological exclusion takes the position that biology is destiny. But from an economist's perspective, this strict biology-based hypothesis is not completely satisfactory for at least two reasons.[3] First, an identification problem exists. It is impossible to determine precisely which biological, physiological, or technological differences might have led to the Neanderthal's demise. Physical differences existed between early man and the Neanderthal. But few reasons emerge to believe the two species were all that different anatomically. Neanderthals were slightly more squat and broad, but each species was strong and clever, and had the ability to develop tools and weapons (see Gee 1996, Bahn 1998, Mellars 1998, Bergeron 1999).[4] And even if significant differences existed between the two species, science does not know for certain that these differences favored

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[2] Several theories are based on physical differences. One thesis is that Neanderthals had a greater instance of fatal complications during childbirth due to their larger craniums (Guk 1997). Another idea is that Neanderthals were better suited to a cooler climate and were somewhat less suited than humans to the warmer climates after the glacial icesheets retreated. However, it is incorrect to infer that Neanderthals were *best*-suited for a cool climate or that they were unable to adapt to different climates. Neanderthals had successfully adapted to several periods of climate change, which has led some to discount this theory (Tattersall and Schwartz 2000).

[3] Also see for example Shogren and Crocker's (1999) discussion on endogenous actions to control risk, and 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.

early man. Neanderthals supposedly had superior bodily strength and presumably were well-adapted to the harsh biophysical environment in which they lived for thousands of years. Finally, Diamond (1992) writes that Neanderthals had 10% larger brains than humans, which does not necessarily imply they were smarter—although that cannot be ruled out. So what exactly was it about the biology that triggered early human dominance over the Neanderthal?

Second, the biological exclusion principle is not entirely satisfactory because it is based solely on the traits of individual members of a population. Ever since Darwin, biologists have been prone to consider what is beneficial or costly for the *individual organism* (i.e., its birth and death rate, or ability to find food and tolerate stress), not the group of individual organisms. Efforts to translate the theory of natural selection to the group level are often treated with extreme suspicion, and are believed to stretch evolutionary biology theory beyond reasonable limits (e.g., Wynne-Edwards 1962). This paradigm may have affected thinking about other biological theories, like those pertaining to biological exclusion. But while the focus on individuals and the credo "nature does not look forward" (e.g., Eldredge 1995) may be correct for non-sentient beings as squirrels, it does not help in understanding the dynamics of human society (notwithstanding advances in sociobiology, see chapter 20 in Wilson 1975).[5] Humans can create and commit to exchange institutions that promote trade and insurance, and may organize themselves to reap the gains from trade that emerge from the specialization of labor.[6]

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[4] Science no longer views Neanderthals as the retarded brutes they were once thought to be.

[5] Darwin originally concluded that humans must have been exempt from natural selection as is believed to occur in the wild. Dobzhansky, who helped introduce Neo-Darwinism, believed that culture exempted humans from traditional notions of evolution. He concluded that culture "precluded the existence of more than one hominid species at any point in time. It just couldn't happen that two species could bear culture" (Tattersall and Schwartz, 2000, p. 32). Science now generally accepts that humans are part of the same evolutionary processes as other species. Our paper shows explicitly how culture may be a part of evolutionary and extinction processes.

[6] Specialization and division of labor can also be seen in nature. For example, specialization in reproduction and other tasks is common in colonies of insects (e.g., bees, ants) and marine invertebrates (e.g., corals). Whether this specialization helped these species to exclude other populations that did not exhibit such behavior is unknown. But because the individual colony members are genetically identical (invertebrate colonies) or at least closely related (insect social systems), the division of labor reflects the common genetic interests and may be rewarded in an

This paper re-examines the early human survival and Neanderthal extinction question from a social or behavioral perspective, whereby individuals collectively develop ways to overcome their individual limits—to make their situation endogenous. Tattersall and Schwartz (2000, p.234) indicate that the key to the problem of coexistence may lie in the "behavioral modernity" of early humans. But no formal theories of the precise behavioral changes, either at the individual or group level, that could have led to Neanderthal extinction have been put forth.[7] We consider how the *interaction between individuals* could have caused the difference between species survival. This is based on the notion advanced by Professor Ian Tattersall (personal communication) that modern socio-economic behaviors are expressions of a generalized underlying capacity that was recently acquired and which Neanderthals did not have. As a result, early modern humans experienced endogenous economic advances that led to more products that were more varied and detailed than in Neanderthal and prior human cultures, many more innovations more widely dispersed, and vastly larger social networks than had been developed by previous cultures (Tattersall and Schwartz 2000; Tattersall et al. 1988; Gamble 1999).

Although no single theory is likely to explain all aspects of Neanderthal extinction and the archaeological record is too poorly understood to adequately judge the absolute merits of every theory, we take an initial step at incorporating behavioral responses to economic stimuli. We develop a behavioral explanation of Neanderthal extinction and human survival based on the species' relative ability to capture the gains from trade that arise from the endogenous division of

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evolutionary sense (e.g., Eldredge 1995). Vertebrate societies rarely display such extreme specialization. There is an increasing theoretical literature on cooperation and evolution (Dugatkin 1997).

[7] In the economic literature, Hansson and Stuart (1990) model the gradual displacement of one group of humans by another that behaves economically superior. They model natural selection of stable individual preferences for labor supply and saving, assuming such preferences are heritable traits or passable through learning from parents, and that selection favors those preferences that maximize the sustainable number of offspring. Their model, however, is akin

labor. Our model provides an economic underpinning of the competitive exclusion principle at the level of the group, rather than the individual. We find that the development of rudimentary economic exchange institutions—trade and division of labor—could have enabled humans to seal the fate of Neanderthals, even if biology was against them initially.[8]

I. Evidence of Neanderthal stagnation and early human trade

Neanderthals originated about 300,000 B.P. and occupied much of Europe and West Asia by up to 200,000 B.P. To put this in perspective, they survived as a species for longer than humans have been around. The archaeological evidence does not support the concept of division of labor and trade, at least not in a meaningful economic way relative to the human groups that followed.

Gamble (1999) classifies Neanderthal society as complex – a term he also uses to describe baboon societies, at least in terms of their social networks. Social group sizes were relatively limited, consisting of about two-dozen individuals at most, and the living spaces of these individuals were largely unorganized, with no evidence that the spaces were divided according to different functions (Tattersall and Schwartz 2000). Tattersall and Schwartz (2000, p.212) indicate "…there is little evidence to refute Binford's notion that the Neanderthal's lacked modern human levels of forward planning and anticipation. Certainly, the sites lacked the structure and complexity of those of early modern humans, and it is reasonable to suppose that this reflects a fundamental difference in lifestyle." Neanderthal technologies did not advance significantly over their long reign, which has been interpreted as evidence of a lack of competition and social interaction (Kuhn and Stiner 1998), particularly inter-group interactions

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to the biological exclusion principle literature as the results are driven by differences in individual characteristics distributed in a nondegenerate fashion among homogenous 'clans'.

[8] The term trade is used for clarity and convenience. However trade, which is typically defined as voluntary exchange, is not necessary for the results we obtain. Instead, all that is needed is a division of labor and some mechanism for exchange – be it voluntary or involuntary (e.g., centralized planning by a dictator).

(Gamble 1999).

This view is also supported by evidence that raw materials were not often transported and any transportation that did occur was over relatively small distances (Gamble 1999). Neanderthal groups remained somewhat isolated, not ranging far from home. They did not develop meaningful trade links with other Neanderthal groups (Gee 1996, p.36). Available evidence suggests that Neanderthals probably cooperated with one another to some extent (Gamble 1999), but does not support the view that specialization arose from any formal division of labor or that inter- or intra-group trade existed. These practices seem to require all the things that Neanderthals lacked—a more complicated social organization, a degree of innovative behavior, forward planning, and the exchange of information, ideas, and raw materials.

Early humans originated in Africa over 100,000 years ago, where they remained for a considerable time. About 47,000 years ago, some humans left Africa to settle in the Levant (the middle east); about 40,000 years ago, other groups left Africa for the Iberian Peninsula. Both groups are thought to possess similar technologies and social structures (Tattersall and Schwartz 2000), although probably more is known about the Iberian humans, first known as the Aurignacians and later the Gravettians (Gamble 1999).

Anthropologists note a major change in society with the advent of humans in Europe and Asia. Gamble states the fundamental difference to be the transition from complex Neanderthal societies to *complicated* human societies, which represent a significant advancement in the complexity of social networks. Unlike Neanderthals, evidence exists that early humans specialized at least to some degree, and that they engaged in both intra- and inter-group trade. They exhibited complex living arrangements in which different sections of the living areas were partitioned for different functions (Tattersall and Scwartz 2000). Moreover, compared to

Neanderthals, early humans developed significantly more types of activities with more detailed workmanship, and they generated more innovations (Tattersall and Scwartz 2000; Blades 2001; Kuhn and Stiner 1998). All of these features are suggestive of specialization. Many innovations were directly related to food procurement (Kuhn and Stiner 1998). A key element in Kuhn and Stiner's (1998) analysis is the link between the incentive to develop new technologies and the potential payoffs from obtaining food surpluses. Many anthropologists have noted how judicious redistribution of excess resources provides a distinct advantage to "efficient hunters", as measured by currency like increased survivorship, social prestige, or reproductive opportunities. For instance, it is believed that killing large game became a method of acquiring wealth, and that efficient hunters could build up "reciprocal obligations" by exchanging food (Mithen 1990).

Describing early humans, Mithen (1990, pp.219-222) states "there can be little doubt that the Upper Paleolithic settlement-subsistence system…was logistically organized with high degrees of scheduling and forward planning." Similarly, Tattersall and Schwartz (2000, p.246) conclude that "Aurignacians lived in social groups much more complex and variable in size than any earlier groups. There is good reason to believe that such 'modern' socioeconomic features such as division of labor and social stratification had already appeared in Aurignacian times."

Evidence also suggests travelling bands of early humans interacted with each other and that inter-group trading emerged. Early humans, the Aurignations and especially the Gravettians, imported many raw materials over long ranges and their innovations were widely dispersed (Tattersall and Scwartz 2000; Blades 2001; Kuhn and Stiner 1998; Gamble 1999). Indeed, "…widespread evidence of long-distance trade in stone, ivory, and fossil and marine shells attest to the social and cognitive complexity of Aurignations to a much greater extent than

in either the Mousterian [Neanderthals] or the Chatelperronian [Neanderthals]" (Tattersall et al., p.64). Such exchanges of goods and ideas helped early humans to develop 'supergroup social mechanisms' (Sahlins 1959). The long-range interchange between different groups both kept "culture going" (Shreeve 1996; Gee 1996) and generated new "cultural explosions" (Pfeifer 1982; Mithen 1998). And as we show in the following discussion, these intra- and inter-group interactions could enable early humans to increase their non-subsistence activities like art, while simultaneously out-competing Neanderthals on their joint hunting grounds.

II. A benchmark model: biological exclusion

A: The basic model

As a comparative benchmark, we begin with a mechanistic biological explanation based on the principle of biological exclusion. The stylised model focuses on the key biological issues. Assume the diets of early man and Neanderthals consisted primarily of meat from hunting (Mosimann and Martin 1975), and they competed for prey.[9]

Imagine a society of humans consisting of *M* households, and a society of Neanderthals, consisting of *N* households. Because our objective is to compare this model of biological exclusion with one of economic exclusion, where within-group trade arises to exploit differences in skills, we go ahead and introduce within-group heterogeneity at this point. Assume members of each population (human and Neanderthal) are in one of two subgroups: (i) *skilled hunters*

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[9] There is perfect niche overlap in our model. It is possible that one evolutionary (or behavioral) response of Neanderthals to competition with humans would have been to change niches. This alternative niche hypothesis does not exist in our model; one future extension would be to allow for this through adding alternative food sources or adding space (see Flores 1998). An anonymous referee points out that if the new niche was associated with greater fluctuations (as limit cycles, chaos, and other forms of complex dynamics can be part of consumer resource systems) than the initial niche which was better-suited for Neanderthals, then even a seemingly minor level of stochasticity could drive Neanderthals to extinction. While biological forces might lead directly to extinction in such a case, the end result would actually be precipitated from the behavioral exclusion of Neanderthals from their initial niche. See Roughgarden (1979, chapter 24) for a discussion of niche theory.

(indexed by *j=s*) and (ii) *unskilled hunters* (indexed by *j=u*). Members of each group primarily sustain themselves by hunting and consuming wildlife, and they also derive utility from 'consuming' a possibly broad set of other goods (e.g., clothes and shelter).[10] Consistent with most of the literature on open access harvesting in primitive societies (e.g. Smith 1975, Brander and Taylor 1998), household utility is a Cobb-Douglas function of meat (*m*) and these other goods (*v*)

(1) $\qquad U_{ij} = m_{ij}^{\beta_i} v_{ij}^{1-\beta_i} \qquad i = M,N; \; j=s,u$

where β_i is a parameter that is not assumed to vary by skill-class. Households maximize (1) subject to a time constraint

(2) $\; l_{ij} = e_{ij} + a_{ij},$

where *l* is the total labor endowment, *e* is hunting effort, and *a* measures effort directed at producing manufactures or other goods. Let *v = a* for simplicity. Harvesting of meat is defined by the standard Schaefer production function (Clark 1990)

(3) $\qquad m_{ij} = q_{ij}e_{ij}x,$

where *x* represents the extant population (biomass) of wildlife and q_{ij} is the *catchability coefficient* defining the ease with which wildlife is harvested. Skilled hunters have a larger catchability coefficient than unskilled hunters, i.e., $q_{is}>q_{iu}$. The parameter q_{ij} may differ between Neanderthals and humans due to differences in hunting efficiency (e.g., physiology).

We assume individuals solve a series of static labor allocation problems rather than a single

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[10]Wildlife serves as a specific proxy for general biological food resources, although meat was heavily consumed during this time. Mosimann and Martin (1975) argue Paleolithic man ate little else than meat; their point is supported by recent research discussed in O'Neill (2002). Throughout we assume that both groups have free access to wildlife resources, with neither group excluding the other's access. See Baker (2003) for an analysis of land tenure in hunter-gatherer societies. Also other goods could include weapons, which would be intermediate inputs into the hunting production function. We do not model these intermediate inputs; we point out the human specialization in these inputs – particularly specialization that leads to technological change—would serve to reinforce our results that trading enables humans to exclude Neanderthals.

dynamic optimization problem.[11] This presumption is consistent both with Mithen's (1990, p.224) observation that "hunter-gatherers do not appear to plan subsistence activities over time scales longer than one year" and with open access resource exploitation (Conrad 1995, Brander and Taylor 1998). Substituting expression (3) into (1), the Lagrangean for an individual of skill level j belonging to population i is

(4) $L = (q_{ij} x e_{ij})^{\beta_i} a_{ij}^{1-\beta_i} + \lambda_{ij}[l_{ij} - e_{ij} - a_{ij}]$.

Solving the problem yields optimal meat consumption,

(5) $m_{ij}^{*} = q_{ij} \beta_i l_{ij} x$,

which is greater when prey is easier to catch, the appetite for meat is greater, the labor endowment is increased, or when wildlife are more plentiful. The functional response is linear in wildlife abundance, x, which stems from Cobb-Douglas preferences and Schaefer harvesting. In Section V we investigate the implications of a nonlinear response.

Population growth (or fertility) in both societies depends on the available food supply, which is particularly true for people living close to subsistence (see Frisch 1978; Hansson and Stuart 1990; Nerlove 1991, 1993; Dasgupta 1995). Following conventional models of predator populations (e.g., McGehee and Armstrong 1977), let the dynamics of the aggregate Neanderthal population be described by

(6) $\dot{N} = N(-d_N + b_N m_N^{*})$,

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[11] We also assume humans and Neanderthals maximize their own utility without considering the effects of their decisions on the "other" society. This implies that neither group makes strategic decisions intended to wipe out the other group. This assumption matters because ultimately the *relative* well-being of the two groups drives our results; a society aware of this situation has a strategic advantage in out-competing the other society (Kockesen *et al*. 2000). At least three requirements must hold for such strategic actions to occur. First, strategic actions require a 'theory of mind'—an ability to attribute states of mind to others so as to predict their actions (see Robson 2001). Second, a finite discount rate is required since the strategy can only be successful in the long run, possibly thousands of years. Third, the group must work together to achieve a common goal—the maximization of social net benefits for the group. In the absence of evidence that any of these conditions were satisfied for Neanderthals or early

where d_N is the mortality rate, $b_N m_N$ is the birth rate, and m_N is average per capita meat consumption. The population shrinks (grows) whenever average household meat intake falls short of (exceeds) a subsistence level, S.[12] The parameter b_N is set equal to d_N / S_N, where S_N represents the minimum quantity of food that Neanderthals need to support themselves. From expression (6), if $m_N / S_N < 1$, the population growth rate is negative and the population diminishes. As $m_N / S_N \rightarrow 1$, the population does not change. If $m_N / S_N > 1$, the population grows. Population growth for humans has an analogous specification, which is obtained by substituting M for N in equation (6)

(7) $\dot{M} = M(-d_M + b_M m_M^*)$.

We modify Neanderthal population growth relative to (6) to account for the heterogeneous sub-populations, although growth of one sub-population can depend on the other. We assume the offspring of skilled hunters can be either skilled or unskilled; unskilled hunters can have either skilled or unskilled offspring. Denote the proportion of skilled hunters' offspring who are also skilled by η_{Ns}; and the proportion of unskilled hunters' offspring who are unskilled by η_{Nu}. Heredity is likely to bias the distribution of offspring's skills along the lines of parentage, such that $\eta_{Ns} > 0.5$, $\eta_{Nu} > 0.5$. The skilled sub-population grows according to[13]

(8) $\dot{N}_s = N_s(-d_N + \eta_{Ns} b_N m_{Ns}^*) + N_u(1 - \eta_{Nu}) b_N m_{Nu}^*$

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humans, we abstract away from such strategic interaction. If early humans did possess mental faculties to engage in strategic interaction with Neanderthals whereas Neanderthals did not, the main results of this paper are reinforced.

[12] Strauss and Duncan (1998) discuss the importance of such thresholds.

[13] This specification accounts for innate skills and does not address the possibility that those with fewer innate skills could learn from more-skilled hunters. To incorporate learning would significantly complicate the model and would require keeping track of which skilled hunters had innate versus learned skills (Cavelli-Sforza and Feldman, 1981). Another issue might be the time devoted to education and learning, since the time allocation is finite. Boyd and Richerson (1985, particularly chapters 4 and 6) and Cavelli-Sforza and Feldman (1981) for parent-teacher models of cultural transmission. With specialization and trade, one could argue that humans had the comparative advantage in education too, which would again serve to accentuate our results.

Growth of the unskilled sub-population is defined by switching the *s* and *u* subscripts in (8). Growth of the skilled and unskilled human sub-populations is also analogously defined.

Let ρ_i represent the proportion of skilled hunters in population *i*. This proportion may change over time in response to fertility and mortality in each subgroup. The evolution of ρ_i is driven by natural selection, which is distinct from competitive exclusion. Competitive exclusion involves one distinct population displacing another population, whereas natural selection involves changes in genetic traits within a population interacting with its environment. 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 will ultimately change the population's composition. We define the *rate of natural selection,* for instance in the human population, by $\dot{\rho}_M / \rho_M = (1 - \rho_M)(\dot{M}_s / M_s - \dot{M}_u / M_u)$. Natural selection favors skilled humans when $\dot{\rho}_M / \rho_M > 0$; it favors unskilled humans when $\dot{\rho}_M / \rho_M < 0$. The selection rate is defined analogously for Neanderthals: selection favors skilled or unskilled Neanderthals when $\dot{\rho}_N / \rho_N > 0$ or $\dot{\rho}_N / \rho_N < 0$.

Using expression (8) along with meat consumption levels for each sub-group, the rate of natural selection for humans is (with an analogous rate applying to Neanderthals)

$$(9) \quad \frac{\dot{\rho}_M}{\rho_M} = \{[\eta_{Ms} q_{Ms} - \eta_{Mu} q_{Mu}] - [(1 - \eta_{Ms}) q_{Ms} \frac{\rho_M}{1 - \rho_M} - (1 - \eta_{Mu}) q_{Mu} \frac{1 - \rho_M}{\rho_M}]\}(1 - \rho_M) b_M \beta_M l_M x$$

The relevant tradeoffs occur within the bracketed ({}) term on the right hand side of expression (9). The terms $\eta_{Mj} q_{Mj}$ (*j=s,u*) represent a sub-population's *own-fertility effects* – the direct fertility effects a sub-population has on its own sub-population. The terms $(1 - \eta_{Mu}) q_{Ms} \rho_M / (1 - \rho_M)$ and $(1 - \eta_{Ms}) q_{Mu} (1 - \rho_M) / \rho_M$ 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 Appendix I, we show that the proportion of skilled hunters, ρ_i, converges monotonically over time to a unique value, ρ_i^*. For instance, starting with a small proportion of skilled hunters, the proportion increases monotonically over time until the steady state is reached. Once $\rho_i = \rho_i^*$, the proportion of skilled hunters remains constant, regardless of changes in the competing homonid population or the prey base.

Consider now the prey of human and Neanderthal hunters. We combine all wildlife populations into a single aggregate variable x, ignoring any changes in species composition over time. Wildlife growth is governed by the conventional logistic growth function

(10) $G(x) = \alpha x(1 - x/k)$,

where α is the intrinsic growth rate and k is the carrying capacity. Human and Neanderthal harvests reduce wildlife growth, and so the dynamics of the wildlife stock are described by

(11) $\dot{x} = \alpha x(1 - \dfrac{x}{k}) - Nm_N^* - Mm_M^*$.

For this model, small differences in one or more of the 'biological' parameters $q_i, l_i, \beta_i,$ or S_i lead to the extinction of the slightly less accomplished "predator" species (see Appendix I).[14] Humans survive if they have some combination of greater hunting efficiency, preferences for meat, time available for work, or lower subsistence requirements relative to

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[14] We have not mentioned how differences in d might affect extinction because d has a dual impact under the current specification (since $b=d/S$). For a larger d, population growth is greater when the population is nourished, and population decline is greater when the population is malnourished. In addition, differences in preference parameters

Neanderthals; or vice versa. We illustrate this with a numerical example based on a discrete approximation of the model and calibrated using data on megafauna harvesting from Whittington and Dyke (1984) (see Appendix II for specifics). The following parameter values serve as a benchmark for both Neanderthals and humans: $S = 2.9$ animal units (AU, where 1 AU=1,000 pounds; one grown *Mammuthus imperator* may equal more than 20 AUs.), $d=0.08$, $l=7300$, $k=75$ million AU, $\alpha=0.15$, $\beta=0.6$, $q_{is}=8.3\times10^{-11}$, $q_{iu} = 0.75q_{is}$, and the initial value of $\rho_i = 0.2$ ($i=N, M$).

B: Numerical results

Table 1 shows the results for cases in which humans are more biologically efficient: the parameters q and l are three percent larger and S is three percent smaller for humans.[15] In each case, assume a small group of humans enter after Neanderthals have reached an equilibrium with the wildlife population, which is consistent with local Neanderthal populations living for up to hundreds of thousands of years before humans arrived. The results in Table 1 indicate human survival and Neanderthal extinction—an example of biological exclusion as discussed by many others and modelled, for example, by Flores (1998).

Although the biological efficiency differential (e.g., Δq) is arbitrarily chosen, the predicted extinction intervals correspond well with Flores' (1998, p.295) claim that the "massive extinction was completed between 5,000 and 10,000 years, depending on the region." Pettitt (1999), however, argues that local extinction events may have occurred more rapid—within about 30 generations, or some 600 years. His elaborate discussion of the difficulties associated with carbon dating such brief periods does not bode well for more accurate predictions of the extinction interval in the future. In what follows we therefore focus on the qualitative results and

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such as β could lead to extinction of one species. This result would support the principle of biological exclusion, particularly to the extent that preferences have biological foundations (see Robson 2001).
[15] Smaller differences produce similar results, the only difference is that it takes more time.

refrain from discussing our predicted intervals in detail since there is no reasonable context in which to place these numbers.

Figure 1 illustrates the dynamics of the extinction process for the case in which humans are more efficient hunters. The superior hunting ability of humans implies a slow displacement and eventual extinction of Neanderthals. Prior to human arrival, the Neanderthal and wildlife populations are in equilibrium with wildlife abundance at about 9 million AU and a Neanderthal population of about 375,000. In year 0, a small population of humans settles in Neanderthal territory. The human population grows given the relative abundance of wildlife. Human hunting, however, causes a slight decline in the wildlife population and the diminished wildlife stock can no longer support the existing Neanderthal population. Human population-growth and Neanderthal population-decline occur monotonically as humans replace Neanderthals.

Recall the outcome of Neanderthal extinction and human survival is reversed if we assume humans were biologically less efficient—a possibility one cannot rule out given the archaeological evidence. If the Neanderthals were biologically more efficient (e.g., better ecologically adapted to the environment in which they survived and gained experience for many millennia), the model predicts humans would not have co-existed with Neanderthals for any significant time interval.[16] But as we demonstrate in the next section, the fact that humans survived and Neanderthals went extinct does not necessarily imply that humans were biologically more efficient. Instead, we demonstrate that humans could have overcome biological inferiorities by increasing their economic efficiency through specialization of labor and inter-household trade.

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[16] When there is a non-linear relation between predators and prey, co-existence of multiple predators (e.g., in the form of periodic orbits or chaotic cycles) may occur in spite of differences in biological parameters (e.g. McGehee

III. A behavioral theory of exclusion

A: The behavioral model

We now turn to our behavioral exploration of Neanderthal extinction. For simplicity and without loss, we focus on the simplest case in which humans engage in a division of labor and trade while Neanderthals do not, although our results would certainly hold if Neanderthals also traded, doing so on a smaller scale than humans. Assume each Neanderthal household produces both the meat and the other goods it consumes; and consumption levels are given by the solution to the static optimization problem in expression (5). We recognize that Neanderthals might have engaged in some inter-household food sharing within their tribe or group (Kuhn and Stiner 1998), as is observed in current hunter-gatherer economies that "smooth" consumption when hunting megafauna (e.g., Kaplan and Hill 1985). Such sharing, however, would have been limited to small groups – immediate family and close allies. Moreover, food sharing need not have evolved towards more external trading and specialization of tasks, as supported by the evidence of a stationary and isolated Neanderthal culture. Even if we allowed for the possibility of within-group Neanderthal trade, the gains from trading and specialization for humans trading *within* and *between* groups would still have been greater.

Assume humans organize and specialize such that they engage in inter-household trade (see Sahlins 1974 for an interesting anthropological account of trade, including various constraints among 'modern' primitive cultures). Each household makes labor allocation decisions to maximize utility (1) subject to the budget constraint[17]

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and Armstrong 1977). We examine several non-linear models in Section V and find this does not occur in our specifications.

[17] In general, trading could also increase the quality of goods used by some humans, which could affect q over time for both skilled and unskilled hunters. For instance, humans might import better quality raw materials for tools and weapons, or these products may be improved through technical change stimulated by trade. While we do not model these processes explicitly, their inclusion would reinforce the results of this paper.

(12) $m_{Mj} + p v_{Mj} = q_{Mj} e_{Mj} x + p(l_{Mj} - e_{Mj})$ $j = s, u$

where p is the price of other goods in terms of meat. Since the first order and market clearing

conditions for such optimization problems are well known and straightforward, we do not derive

them here. Instead, Table 2 summarizes the resulting trading equilibria, which we now discuss.

Using this Ricardian model, we find that three possible equilibria emerge depending on

the relative scarcity of skill levels within the human population (Krugman and Obstfeld 1991;

Chacholiades 1978). Under Scenario A in Table 2, skilled human hunters are scarce and their

within-group comparative advantage in hunting (i.e., q_{Ms} / q_{Mu}) is relatively small. Skilled

hunters only hunt, and the unskilled hunters do both—they make other goods and they hunt.

This variation results in the same amount of meat consumption as in the no-trading equilibrium

and a greater consumption of other goods by skilled hunters (Table 2). Skilled hunters benefit

from this division of labor because the relative price of the other good falls—they do not need to

spend time to produce them. The change in relative prices, however, does not cause them to

consume any additional meat because of the offsetting income and cross-price effects that arise

with a Cobb-Douglas function. With Cobb-Douglas, if the price of the other good falls, the

skilled hunters only consume more of the other good. The net result does not increase the

fertility of humans relative to Neanderthals.[18]

Scenarios B and C tell a different story (see Table 2). Scenario B involves complete

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[18] This result follows from our assumption that fertility is a function of meat consumption only (see O'Neill 2002). It might be equally valid to assume that consumption of "other goods" (shelter, etc.) also affects replenishment, i.e., growth of the human and Neanderthal populations might be more appropriately modeled as a function of utility (fitness) as opposed to just meat. We do not pursue such an analysis here because of the difficulties associated with inter-personal (species) utility comparisons and because the associated nonlinearities would make it difficult to produce clear analytic results (McGehee and Armstrong 1977). Were we to model population growth as a function of utility, our results would only be enhanced because trading would then increase population growth along two dimensions – meat and other goods – as opposed to the single dimension of the present model. Finally, note that like the skill level in society, preferences could have been shaped by natural selection (Robson 2001, Rogers 1994, Stuart and Hanson 1990). Within scenarios we hold preferences (β) constant to keep the model tractable.

specialization—skilled hunters hunt; unskilled hunters produce the other goods. Skilled hunters benefit because the relative price of other goods falls. With unskilled hunters specializing in their comparative-advantage activity, they obtain meat at a lower cost than in Scenario A or the no-trade case. Their meat consumption goes up. A similar result arises in Scenario C but for a different reason. Here skilled hunters produce both meat and other goods because their numbers are plentiful; the unskilled hunters only make other goods. The skilled hunters do not benefit from trade because the relative prices they face have not changed from the no-trading case. The unskilled hunters do benefit, however. Since unskilled hunters again specialize on other goods, the skilled hunters still devote more time to hunting and produce more meat than would be produced under no-trading or Scenario B. All extra meat goes to unskilled hunters.

In Scenarios B and C, trade has a non-negative impact on meat consumption for each group, with at least one group consuming more. The net effect is an increase in the growth rate of the human population relative to Neanderthals. We now explore how this increased population growth affects natural selection, the scarcity of skill levels and the type of trading system that emerges, and species exclusion.

B. Natural selection, trade, and exclusion

From Table 2, we see that the evolution of ρ_M —the proportion of skilled human hunters—is the key variable that determines which trading scenario emerges at different points in time. As described above, the evolution of ρ_M is driven by natural selection. For trading Scenario A, natural selection occurs according to equation (9) for the no-trading outcome described above – driven by both own-fertility and cross-fertility effects. Note that human meat consumption

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Incorporating the selection of preferences would require an additional source of within-species heterogeneity, defined according to utility.

patterns here are identical to the Neanderthal, which means this discussion of Scenario A also applies to the no-trade scenario adopted by Neanderthals.

With trading Scenarios B and C, additional *indirect fertility* effects emerge. Consider first Scenario B—the complete division of labor scenario. Here the rate of natural selection expression analogous to expression (9) is

(13)

$$\frac{\dot{\rho}_M}{\rho_M} = \{[\eta_{Ms}q_s - \eta_{Mu}q_s \frac{\rho_M}{1-\rho_M}\frac{1-\beta_M}{\beta_M}] - [(1-\eta_{Ms})q_s \frac{\rho_M}{1-\rho_M} - (1-\eta_{Mu})q_s \frac{1-\beta_M}{\beta_M}]\}(1-\rho_M)b_M\beta_M l_M x$$

The productivity of a skilled human hunter has (i) a direct effect on the fertility of both his own sub-population and the unskilled hunters, and (ii) an indirect effect due to the complete division of labor—meat consumption of unskilled hunters depends on the productivity of the skilled hunters. More productive skilled hunters relative to unskilled hunters enables the unskilled population to consume more meat and increase their fertility relative to Scenario A and the no-trading scenario. The indirect fertility effects positively affect the own- and cross-fertility effects of unskilled hunters, which benefits both sub-populations. Assuming $\eta_{Mu} > 0.5$, the own-fertility effect of unskilled hunters dominates the cross-fertility effect. Additional consumption of meat by unskilled humans relative to skilled humans implies that trading reduces the forces that drive natural selection. A similar story can be told for trade Scenario C.

In Appendix I, we show that ρ_M evolves monotonically over time until an equilibrium value is achieved, after which point ρ_M remains constant for all future periods. An equilibrium emerges for only one trading scenario, although other trading scenarios can emerge en route to the equilibrium scenario. In Appendix I, we also show that under Scenarios B and C the division of labor reduces the forces driving the natural selection of skilled hunters. This ultimately results

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in a relatively greater selection of skilled hunters within the Neanderthal population, $\rho_N > \rho_M$.
Trade reduces the average skill level in human society.

We have shown that natural selection affects the relative scarcity of skilled hunters and the emergent trading scenario, and that the trading scenario in turn affects the rate of natural selection. We now define our *behavioral exclusion principle* between humans and Neanderthals. Appendix I shows this principle arises given identical biological parameters across species and provided that humans do not get stuck in Scenario A. Behavioral exclusion occurs if per capita meat consumption of humans exceeds Neanderthal consumption, which is formally represented by the following condition

$$(14)\ \rho_M(m_{Ms}^* - m_{Ns}^*) + (1-\rho_M)(m_{Mu}^* - m_{Nu}^*) - \delta(m_{Ns}^* - m_{Nu}^*) = \Omega - \Delta > 0$$

where $\delta = \rho_N - \rho_M$, $\Omega = \rho_M(m_{Ms}^* - m_{Ns}^*) + (1-\rho_M)(m_{Mu}^* - m_{Nu}^*)$, and $\Delta = \delta(m_{Ns}^* - m_{Nu}^*)$. The term Ω represents how gains from trade affect increased per capita meat consumption and exclusion, holding natural selection constant. The term Δ offsets exclusion since $\delta > 0$ due to the greater natural selection of skilled hunters within the Neanderthal population ($\rho_N > \rho_M$).

In Scenarios B and C, humans exclude Neanderthals because human per capita meat consumption is greater due to the division of labor. Skilled humans consume the same amount of meat as their Neanderthal counterparts while unskilled humans consume more, such that $\Omega = (1-\rho_M)(m_{Mu}^* - m_{Nu}^*) > 0$. Natural selection within the Neanderthal population, however, partially offsets the gains from the division of human labor since $\Delta < 0$.[19] This is because a larger value of ρ_N relative to ρ_M reduces the per capita meat consumption advantage that trading humans have relative to Neanderthals. Neanderthal exclusion still occurs, however, as

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long as all biological parameters are identical across the species (see Appendix I) – exclusion just takes longer than if natural selection was not a factor. But if biological factors did significantly favor Neanderthals, this natural selection effect ($\Delta < 0$) could make Neanderthal exclusion less likely, or even trigger the exclusion of humans.

Below we illustrate the behavioral exclusion principal numerically. The benchmark parameter values are adopted..[20] Tables 3 and 4 report the results for various combinations of values for η_{is} and η_{iu} ($i=N, M$), maintaining $\eta_{Ms} = \eta_{Ns}$ and $\eta_{Mu} = \eta_{Nu}$ such that trade is the only factor influencing exclusion.

C: Numerical results with equal biological efficiency

Table 3 presents the simulation results assuming equal biological efficiency of humans and Neanderthals. The results confirm our expectations. With no biological differences, trading humans survive and non-trading Neanderthals go extinct, provided η_s is not too small and η_u is not too large relative to η_s; otherwise trading Scenario A emerges and co-existence results. Comparing fertility scenarios 1 and 2 shows how the division-of-labor boosts the power of behavioral exclusion. A 25 percent reduction in η_{iu} ($i = M, N$) cuts the Neanderthal extinction time by more than half. Although both populations experience greater selection of skilled hunters relative to fertility scenario 1, the shorter extinction time occurs despite greater selection of skilled Neanderthal hunters (i.e., $\rho_N > \rho_M$). The difference must be due to trading. The reduced relative scarcity of skilled human hunters allows humans to attain trading Scenario C, in which unskilled hunters consume even more meat, while skilled hunters do not consume any

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[19] Among Neanderthals, food sharing that is unaccompanied by a division of labor would not increase per capita meat consumption, but it would decrease the natural selection of skilled Neanderthals since they would eat less under a sharing system. Neanderthal food sharing would therefore speed up the exclusion process.

less. Natural selection of skilled hunters has a greater impact when a division of labor exists.[21]

The behavioral exclusion process is virtually identical to the biological exclusion process in Figure 1, except for the time frame. In year 0, Neanderthals are in equilibrium with $\rho_N = 0.6$ (a proportion maintained throughout the exclusion process).   Humans enter Neanderthal territory with $\rho_M = 0.2$. Humans begin trading according to Scenario A since skilled human hunters are scarce. But over time skilled hunters become less scarce. After 56 years, natural selection has increased the proportion of skilled human hunters to $\rho_M = 0.53$ to allow for a complete division of labor. Humans retain this division of labor until Neanderthals go extinct, with ρ_M increasing to 0.56 over the following 180 years. Even with a higher proportion of skilled hunters, Neanderthals cannot compete against the humans' economic system.

C. Results with unequal biological efficiency

What if the Neanderthals were more biologically efficient than humans?   Table 4 shows that conditions exist such that economic efficiency can overcome this biological advantage. Suppose the catchability coefficient, q, is 5 percent larger than the value used in Table 3, for both skilled and unskilled Neanderthals. Under fertility scenario 1, human division of labor is insufficient to overcome the greater biological efficiency of Neanderthals. Humans can only withstand up to a 3 percent differential. This value increases to 7 percent under fertility scenario 2. The results are identical for a larger l or a larger β (and similar for a smaller S) by Neanderthals because each of these parameters has the same marginal impact on Neanderthal meat consumption.

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[20] The choice of $\rho_M = 0.2$ has little bearing on the results.

The results are markedly different when we consider fertility differences between Neanderthals and humans in Table 4. Increased Neanderthal fertility rates favoring skilled hunters generally have only a small effect on offsetting behavioral exclusion. For instance, under human fertility scenario 2, even runaway natural selection within the Neanderthal population is inadequate to overcome greater human economic efficiency. A homogeneous group of skilled Neanderthals would have to exist to overcome behavioral exclusion, which seems unlikely based on available evidence.

V. Alternative specifications

In Table 3, we explored how different assumptions about fertility rates affected the basic results. We now consider five alternative parameter specifications that could also affect the results: the environmental carrying capacity of wildlife, which impacts human and Neanderthal carrying capacities and roughly corresponds to the available land area under consideration; the intrinsic growth rate of wildlife; the degree of comparative advantage held by skilled hunters (q_s / q_u); the elasticity of substitution of goods in the utility function; and congestion externalities on the hunting grounds. [22] Table 5 reports the results using fertility scenario 1 from Table 3 as the base

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[21] Comparison of fertility scenarios 1 and 3 shows a 25 percent reduction in η_{is} ($i = M, N$) pushes natural selection in the opposite direction. The scarcity of skilled humans is increased and trading Scenario A results. Per capita meat consumption is identical across species and the species co-exist.

[22] Another possible extension, which we do not consider, concerns the relation between nutrition and productivity. Hunting megafauna relies on strength and endurance, which depends on good health and nutrition. Caloric intake is associated with increases in maximum oxygen intake, and therefore with fitness (e.g., Dasgupta 1993, Strauss and Duncan 1998). Even if q_j ($j = s, u$) was the same across species, one could assume "effective productivity" might be greater in one species due to better nutrition. Capturing this idea is beyond our current scope, in part because the number of sub-groups would grow too rapidly over time to monitor (e.g., a skilled hunter having unskilled parents may have a different nutritional status than a skilled hunter having skilled parents, etc.). One can speculate as to how this extension might affect our general results. Increased meat consumption may cause skilled humans to develop both a productivity and fertility advantage relative to skilled and unskilled Neanderthal hunters. These effects could be reinforcing over time. In contrast, Neanderthal fertility and nutrition, and productivity might be diminished in subsequent periods as the combination of human and Neanderthal harvests reduce the wildlife stock. The relatively greater nourishment and productivity of humans, combined with the lack of nourishment and productivity of Neanderthals, effectively increases the relative biological efficiency of humans. Positive feedbacks exist between productivity and consumption, which enhance the humans' comparative advantage created by their

model of comparison.

First, suppose we reduce the environmental carrying capacity, *k*, by 50 percent. Table 5 shows this reduction has almost no effect on the time to Neanderthal extinction, and no effect on the type of trading equilibrium or on natural selection. This result is at least consistent with Pettitt's (1999) findings that periods of human/Neanderthal co-existence may be similar even in regions that vary greatly in size. Similar results hold in the second scenario, in which the intrinsic growth rate of the wildlife stock is reduced by 50 percent. Under these first two scenarios, smaller equilibrium predator and prey stocks emerge. Exclusion time is not greatly affected, however: human harvests and fertility are smaller since human harvests depend on a smaller wildlife stock, but there are fewer Neanderthals to replace.

Next suppose skilled humans and Neanderthals have a 50 percent larger comparative advantage to unskilled individuals. Table 5 shows that more comparative advantage cuts Neanderthal extinction time by almost 70 percent. The shorter time frame arises even though natural selection of skilled hunters for the Neanderthal population has increased significantly. Also the increased comparative advantage has not influenced natural selection within the human population—from expression (13), comparative advantage does not influence natural selection because skilled hunters supply all of the meat and their skill level, q_s, has an identical marginal impact on own- and cross-fertility effects of skilled and unskilled hunters.

Fourth, we examine differences in the elasticity of substitution between goods in the utility function, denoted σ. Consider the CES utility function $U_{ij} = (\beta_i m_{ij}^{\theta_i} + (1-\beta_i) v_{ij}^{\theta_i})^{1/\theta_i}$, where $\theta_i = (\sigma_i - 1)/\sigma_i$. Cobb-Douglas utility is a special case of CES utility in which σ=1. One

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trade-induced superior economic efficiency (see Strauss and Duncan, 1998). These feedback loops may also preclude a Neanderthal comeback should this species start to mimic the trading behavior of humans.

consequence of the σ=1 restriction is the canceling out of the income and cross-price effects associated with a decrease in the price of other goods (v). The result is skilled humans always consume the same amount of meat as they would in the no-trade scenario (see Table 2). A second consequence is the meat consumption function is linear in the resource stock.

Since both consequences vanish when σ≠1, we now let σ equal a value other than unity. For instance, optimal meat consumption under the no-trading equilibrium (or trading Scenario A) is given by the nonlinear response

$$(15) \qquad m_{ij}^* = \frac{q_{ij} x l_i}{1 + (\frac{\beta_i}{1-\beta_i})^{\frac{1}{\theta_i - 1}} (q_{ij} x)^{\frac{\theta_i}{\theta_i - 1}}}$$

The relation is more complex under trading Scenarios B and C.

If σ<1, the goods are net complements. When humans gain from trade, the income and substitution effects no longer cancel and individuals adjust their consumption package in response to changing relative prices. Depending on the trade scenario that emerges, this suggests skilled humans consume more meat (Scenarios A and B) than they would in the Cobb-Douglas case, and the natural selection of skilled humans is also increased. Trading also increases unskilled humans' meat consumption in Scenarios B and C, although the increase is smaller than in the Cobb-Douglas case. Trading humans therefore always consume more meat than non-trading Neanderthals, and the final result must be our survival and their demise. Assuming σ=0.8 for the numerical simulation, Scenario A emerges. Unlike Scenario A from Table 2 we now find that skilled hunters consume more meat than skilled Neanderthals, resulting in a gradual process of displacement.

If σ>1, the goods are net substitutes. Depending on the trade scenario that emerges, this suggests skilled humans consume less meat (Scenarios A and B) and that unskilled humans

consume more meat (Scenarios B and C) than they would in the Cobb-Douglas case. Compared to the Cobb-Douglas case, biological exclusion proceeds quickly when trading humans end up in Scenario C: skilled humans consume no less meat and unskilled persons consume even more meat than before. In contrast, humans get excluded when human society gets trapped in Scenario A. Here, per capita meat consumption decreases as skilled humans consume less and unskilled humans consume the same as non-trading Neanderthals, implying humans do not gain the necessary foothold. Finally, in Scenario B it is *a priori* unclear whether humans or Neanderthals will prevail – unskilled humans consume more and skilled humans consume less. Average meat consumption is ambiguously impacted. Regardless of the scenario, however, the depressing effect of trade on the average skill level is more pronounced – the equilibrium value of ρ_M is lower than with Cobb-Douglas utility. We have performed extensive numerical analyses to explore the consequences of CES utility with substitute goods, and found that humans always exclude Neanderthals for the realistic parameter combinations we consider (i.e., Scenario A never arises). Scenario B only arises when $\sigma \leq 1.01$, but even then Neanderthals are excluded. The result in Table 5 describes what occurs if $\sigma = 1.2$, in which human society ends up in Scenario C. The result is rapid displacement of Neanderthals.

Finally, consider the impact of congestion externalities on the hunting grounds. In general, congestion externalities can arise from both intra-specific and inter-specific competition for animals. Hunting congestion typically enters the problem through the harvest function in the form of diminishing returns to effort (e.g., Clark 1990). We use the following form for individual k of the human population: $h_{kM} = q_{Mj} e_{kM} x (\sum_{s \neq k} z_{MM} e_{sM} + \sum_{s} z_{NM} e_{sN})^{-r}$, where $r \in (0,1)$ is a parameter and $z_{ij} > 0$ if members of population i create congestion externalities for population

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j (*i, j=M,N*); $z_{ij} = 0$ otherwise. This form allows for both intra-specific and inter-specific competition. We define the harvest function for Neanderthals analogously.

The key questions are: does hunting congestion affect human populations more than Neanderthals, and what are the implications for exclusion? For non-trading hunters and given Cobb-Douglas utility, it is straightforward to show that meat consumption is inversely related to the number of "other" hunters, e.g., $m_{kM} = q_{Mj}x(\beta l)^{1-r}/(z_M[M-1]+z_N[N-1])^r$ in the human case. The relations arising in our trading equilibria are qualitatively similar in this regard. We investigate the impact of congestion externalities numerically, assuming $z_{ii} = 1$ and $z_{ij} < 1$ (*i, j=M,N*) in accordance with the view that intra-specific competition created larger congestion externalities than inter-specific competition (e.g., because humans and Neanderthals did not cross paths too much). Table 5 presents the results for several parameter combinations. The results suggest that externalities tend to delay exclusion, although Neanderthals still eventually go extinct. We do find, however, some extreme cases (not reported) in which extremely prolonged co-existence might result. Two factors drive these extreme cases: (1) humans have more difficulty establishing themselves when confronted by Neanderthal-created externalities; and (2) if $z_{ij}<1$, as Neanderthal populations fall, Neanderthals face smaller congestion problems within their own population, which in turn reduces the pace of exclusion.[23]

V. Concluding remarks

Stephen Jay Gould once argued that the current dominant position of *Homo sapiens* on this planet is not the inevitable outcome of a purposeful evolutionary process. Rather, our rise to

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[23] In contrast, when we ignore inter-specific competition there are also cases where congestion *accentuates* our main results (for high or intermediate densities of both humans and Neanderthals). Trading and specialization may reduce congestion externalities for humans (in those scenarios where trade causes a re-allocation of labor towards the

power depended on an exceeding number of exogenous factors including the Cambrium explosion, comet and meteor hits and the demise of dinosaurs, leading Gould to conclude that we are a "wildly improbable evolutionary event" (Gould 1989, p.381). If we rewind the tape of history and run it again, he wrote, the chance of human domination is exceedingly small. This paper demonstrates that the fate of humanity may have been even more uncertain—even on the current and improbable trajectory leading to human domination, interaction with contemporary rivals some 40,000 years ago could have been fatal to humanity. We did not enter a vacant niche in ecological system—we had to conquer it.

But just how did we conquer and rise to dominance? Many theories attempt to explain the rise of humanity in Eurasia and the associated Neanderthal extinction in terms of biology or aggression. Although no single theory is likely to be a Panacea and nobody really knows which theories, if any, are correct, a significant limitation of existing theories is that they tend to abstract away from behavioral responses to economic stimuli. Economic forces have played integral roles in shaping societies throughout recorded human history, and there is no reason to discount either the presence or potential impact of economics in the pre-historic dawning of humanity.[24] Economics might have been the only thing going for us in those early days – even though these forces may have to some extent conflicted with biological forces. We conclude that humans would always prevail if humans and Neanderthals were about equally capable and humans 'invented' the appropriate economic institutions. Humans could have conquered their niche even if the incumbent party was somewhat stronger or better adjusted to its environment. Based on these findings, we conclude that a behavioral basis and endogenous choices may exist

production of other goods), enhancing their ability to outperform Neanderthals. Trade can thus make a non-linear response function "more linear." We would like to thank a referee for pointing this out.

[24] For example, an alternative economic theory of Neanderthal extinction may be based on Diamond's observation that early humans lived some 20 years longer than Neanderthals (Diamond 1992). In a society without writing,

for the eventual rise of human domination, although we should emphasize that there was nothing inevitable about it. We believe the behavioral model strengthens Gould's claim that our existence is improbable.

A crucial issue remains unresolved—it is an open question why the early humans first realized the competitive edge from trade. Some attribute this edge to differences in cognition or language abilities or both, but the jury is still out (Tattersall and Schwartz 2000; Mithen 1990). While this may seem to lead back to biology, genetic differences do not necessarily make an individual more competitive in the acquisition of resources. Rather these biological differences facilitate group interaction, which in turn brings more success to the group as a whole. A natural starting place to address the origin of rich social structures involving trade in future work is to examine the two competing theories that explain the development of rationality: *social intelligence theory* — strategic interaction with other humans was the key to evolving rationality, in which longevity and rationality go hand in hand (see Robson 2001); and *ecological intelligence theory* — interactions with the environment triggered the development of rationality. The ecological theory gives rise to a tantalizing possibility. Akin to findings in the "induced innovation" literature, humans may have had more incentives to "invest in rationality" (Robson 2001) if their level of biological efficiency was low. Obviously this development of rationality took place before humans entered the Eurasian battleground studied here. If this was the case and if trading emerged as a solution, their relatively biological inefficiency effectively stimulated trade. Here the differences between our behavioral model and models of biological exclusion are even starker: it might have been their biological inefficiency that stimulated efforts to make humans more economically efficient and that saved them. Exploring whether the ecological

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accumulation of knowledge is based on one generation teaching the next, so that longevity facilitates the accumulation of social capital (see also Kremer 1993). Exploring the details of this model is left for future research.

theory or the social theory or some combination can capture this outcome seems worthy of future

attention.

References

Baker, M.J., 2003. An equilibrium model of land tenure in hunter-gatherer societies, *Journal of Political Economy*, In Press.

Bahn, P.G., 1998. Neanderthals Emancipated, *Nature* 394, 20 August: 719-720.

Bergeron, L., 1999. Give them Credit for Some Brains, *New Scientist*, February 6: 23.

Bergstrom, T.C., 1996. Economics in a Family Way, *Journal of Economic Literature* 34: 1903-1934.

Blades, B.S., 2001. *Aurignacian Lithic Economy: Ecological Perspectives from Southwestern France*, New York: Kluwer Academic Publishers.

Boyd, R. and P.J. Richerson. 1985. Culture and the Evolutionary Process. The University of Chicago Press: Chicago.

Brander, J. A. and M.S. Taylor, 1998. The Simple Economics of Easter Island: A Ricardo-Malthus Model of Renewable Resource Use. *American Economic Review* 88: 119-138.

Cavelli-Sforza, L.L. and M.W. Feldman. 1981. Cultural Transmission and Evolution: A Quantitative Approach. Princeton University Press: Princeton.

Chacholiades, M., 1978. *International Trade Theory and Policy,* New York: McGraw-Hill.

Clark, C.W., 1990. *Mathematical Bioeconomics* (2nd ed.), New York: Wiley Interscience.

Conrad, J., 1995. Bioeconomic Models of the Fishery, Chapter 18 in: D. Bromley, ed., *The Handbook of Environmental Economics*, Oxford: Blackwell.

Crocker, T., 2001. Some Economics Questions about the Biology of Biodiversity Protection: Comments on Gibbons, Brown and Layton, and Beissinger and Perrine, in: J. Shogren and J. Tschirhart, eds., *Protecting Endangered Species in the United States: Biological Needs, Political Realities, Economic Choices*, New York: Cambridge University Press.

Dasgupta, P., 1993. *An Inquiry into Well-Being and Destitution*, Oxford University Press.

Dasgupta, P., 1995. The Population Problem: Theory and Evidence, *Journal of Economic Literature* 32: 1879-1902.

Diamond, J., 1992. *The Third Chimpanzee: The Evolution and Future of the Human Animal*, New York: Harper Collins

Dugatkin, L.A., 1997. *Cooperation Among Animals: An Evolutionary Perspective*. Oxford: Oxford University Press.

Eldredge, N., 1995. *Reinventing Darwin: The Great Evolutionary Debate*, New York: Wiley.

Flores, J.C., 1998. A Mathematical Model for Neanderthal Extinction, *Journal of Theoretical Biology* 191: 295-298.

Frisch, R.E., 1978. Population, Food Intake and Fertility, *Science* 199: 22-30.

Gamble, C. 1999. *The Paleolithic Societies of Europe*, Cambridge: Cambridge University Press.

Gee, H., 1996. How Humans Behaved Before they Behaved like Humans, *London Review of Books*, 31 October: 36-38.

Gould, S.J., 1989. *Wonderful Life*, New York: Norton.

Guk, Y., 1997. Why's the Neanderthal Gone? *Science in Russia* 4: 50-54.

Hansson, I. and C. Stuart, 1990. Malthusian Selection of Preferences, *American Economic Review* 80: 529-544.

Hymer, S. and S. Resnick, 1969. A Model of an Agrarian Economy with Nonagricultural Activities, *American Economic Review* 59: 493-506.

Kaplan, H. and K. Hill, 1985. Food Sharing Among Ache Foragers: Tests of Explanatory Hypotheses, *Current Anthropology* 26: 223-245.

Krings, M., A. Stone, R. Schmitz, H. Krainizki, M. Stoneking and S. Paabo, 1997. Neanderthal

DNA Sequences and the Origin of Modern Humans, *Cell* 90: 19-30.

Krugman, P. and M. Obstfeld, 1991. *International Economics: Theory and Trade*, New York: Harper Collins.

Kockesen, L., E. Ok, and R. Sethi, 2000. On the Strategic Advantage of Negatively Interdependent Preferences, *Journal of Economic Theory* 92: 274-99.

Kremer, M., 1993. Population Growth and Technical Change: One Million B.C. to 1990, *Quarterly Journal of Economics* CVIII: 681-716

Kuhn, S.L. and M.C. Stiner, 1998. Middle Palaeolithic 'Creativity': Reflections on an Oxymoron, Chap. 9 in: S. Mithen (ed), *Creativity in Human Evolution and Prehistory*, London: Routledge, pp. 143-164.

McGehee, R. and R. Armstrong, 1977. Some Mathematical Problems Concerning the Ecological Principle of Competitive Exclusion, *Journal of Differential Equations* 23: 30-52.

Mellars, P., 1998. The Fate of the Neanderthals, *Nature* 395, October 8: 539-540.

Mithen, S., 1998 (Ed). *Creativity in Human Evolution and Prehistory*, London: Routledge

Mithen, S.J., 1990. *Thoughtful Foragers: A study of Prehistoric Decision Making*, Cambridge: Cambridge University Press.

Mosimann, J.E. and P.S. Martin, 1975. Simulating Overkill by Paleoindians, *American Scientist* 63: 304-313.

Nerlove, M., 1991. Population and the Environment: A Parable of Firewood and Other Tales, *American Journal of Agricultural Economics* 73: 1334-47.

Nerlove, M., 1993. Procreation, Fishing and Hunting: Renewable Resources and Dynamic Planar Systems, *American Journal of Agricultural Economics* 75: 59-71.

O'Neill, J., 2002. Vital Signs: Nutrition; But What did the Cow have for Lunch? *New York Times*, February 19, Section F, Page 8, Column 4.

Pettitt. P.B., 1999. Disappearing from the World: An Archeological Perspective on Neanderthal Extinction, *Oxford Journal of Archeology* 18: 217-239.

Robson, A.J., 2001. The Biological Basis of Economic Behavior, *Journal of Economic Literature* 39: 11-33.

Rogers, A.R., 1994. Evolution of Time Preference by Natural Selection, *American Economic Review* 84(3): 460-481.

Roughgarden, J. 1979. Theory of Population Genetics and Evolutionary Ecology: An Introduction. Macmillan Publishing: New York.

Sahlins, M.D., 1959. The Social Life of Monkeys, Apes and Primitive Man, *Human Biology* 31: 54-73

Sahlins, M.D., 1974. *Stone Age Economics*, London: Tavistock Publications

Shogren, J. and T. Crocker, 1999. Risk and Its Consequences, *Journal of Environmental Economics and Management* 37: 44-51.

Shreeve, J., 1995, *The Neanderthal Enigma: Solving the Mystery of Modern Human Origins*, Viking.

Smith, V.L., 1975. The Primitive Hunter Culture, Pleistocene Extinction and the Rise of Agriculture, *Journal of Political Economy* 83: 717-755.

Strauss, J. and D. Thomas, 1998. Health, Nutrition, and Economic Development, *Journal of Economic Literature* 36: 766-817.

Tattersall, I. and J.H. Schwartz, 2000. *Extinct Humans*, New York: Westview Press.

Tattersall, I., E. Delson, and J. van Couvering, 1988. *Enclyclopedia of Human Evolution and Prehistory*, New York: Garland Publishing.

Whittington, S.L. and B. Dyke, 1984. Simulating Overkill: Experiments with the Mosimann and Martin Model, Chapter 20 in: P. Martin and R.G Klein, eds., *Quaternary Extinctions: A Prehistoric Revolution*, Tucson: University of Arizona Press.

Wilson, E., 1975. *Sociobiology*, Cambridge: Harvard University Press.

Wynne-Edwards, V., 1962. *Animal Dispersion in Relation to Social Behavior*, Edinburgh: Oliver & Boyd.

Appendix I: Propositions and Proofs

To conserve space, we simultaneously develop propositions and proofs related to both the biological model of section II and the trading model of section III. The trading Scenario A of section III is equivalent to the biological outcome in section II.

***Proposition 1*:** Consider the model of section II, only with homogenous populations (i.e., $\eta_{iu} = 0$ (*i=M,N*). In this model, small differences in one or more of the biological parameters leads to the extinction of the less-accomplished predator species.

***Proof*:** Without loss of generality, we assume humans are biologically more efficient, and we focus on the biological parameters q_i and S_i [from expression (5), a larger value of either q_i, l_i, or β_i has the same effect on meat consumption].

Case 1: $q_M > q_N$. Suppose $l_M = l_N$, $S_M = S_N$ and $\beta_M = \beta_N$, while $q_M > q_N$. Given that $S_N = S_M$, equations (6) and (7) imply that a steady state involving both humans and Neanderthals only arises when $m_N^* = \beta_N q_N l_N x = \beta_M q_M l_M x = m_M^*$. This condition, however, is not satisfied when $q_M > q_N$; instead, $m_N^* < m_M^*$. Using equations (6) and (7) along with $m_N^* < m_M^*$, we find that the following condition must hold

(A1) $\dot{N}/N - \dot{M}/M = b[m_N^* - m_M^*] < 0$

This condition is consistent with four possibilities: (i) *N* and *M* both increase over time, with *M* increasing at a faster proportional rate, (ii) *N* and *M* both decrease over time, with *N* decreasing at a faster proportional rate, (iii) *N* decreases over time while *M* increases over time, and (iv) a cyclical pattern involving possibilities (i)-(iii) develops.

With *x* being a limiting factor on the growth of both *N* and *M*, possibility (i) cannot be sustained. Next consider possibility (ii). With *N* and *M* both decreasing at each point in time, one species eventually goes extinct. Here condition (A1) is only satisfied when *N*→0. Likewise, possibility (iii) degenerates to *N* extinction. Finally, one can show that a cyclical path does not exist (McGehee and Armstrong 1977). We refer the reader to McGehee and Armstrong (1977) for a formal proof as the topological dynamics needed to rule out a cyclical path are beyond the scope of the present paper.

Case 2: $S_N > S_M$. Now suppose $q_M = q_N$, but that $S_N > S_M$ (i.e., humans are biologically more efficient since they require less meat). A steady state involving both Neanderthals and

humans here implies that $m_M^* = S_M$ and $m_N^* = S_N$. Given that $m_N^* = \beta_N q_N l_N x = \beta_M q_M l_M x = m_M^*$, this condition requires that $S_N = S_M$. But this condition is not satisfied since $S_N > S_M$; a steady state involving both species will not arise. Using equations (6) and (7) and given that $S_N > S_M$, the following condition must hold

(A2) $\dot{N}/N - \dot{M}/M = dm^*[1/S_N - 1/S_M] < 0$

The remainder of the proof is identical to arguments presented in Case 1.

Proposition 2. In any no-trading equilibrium, (*i*) a unique equilibrium value of ρ_i exists, denoted ρ_i^*, and (*ii*) ρ_i^* is globally stable (*i=M,N*).

Proof. We present the case *i=N* but note the results also hold for *i=M*. The rate of natural selection in the no-trading scenario is given by equation (9). From (9), an equilibrium (steady state) for ρ_N occurs when either $\rho_N = 1$ or when the following condition holds

(A3) $[\eta_{Ns} q_s - \eta_{Nu} q_u] - [(1 - \eta_{Ns}) q_s \dfrac{\rho_N}{1 - \rho_N} - (1 - \eta_{Nu}) q_u \dfrac{1 - \rho_N}{\rho_N}] = 0$

Since $\rho_N = 1$ is impossible when $\eta_{Nj} < 1$ (*j=s,u*), an equilibrium can only occur when condition (A3) is satisfied. Denote the first bracketed term ([]) on the LHS of (A3) by χ and the second bracketed ([]) term by $\xi(\rho_N)$, which is strictly increasing in ρ_N. Note that $\xi(1) > \chi$, and $\xi(0) < \chi$. By the intermediate value theorem, there exists a unique value $\rho_N^* \in (0,1)$ such that $\xi(\rho_N^*) = \chi$. This proves part (*i*).

Condition (A3) does not depend on any variables that change over time, other than ρ_N. Once ρ_N^* is attained, condition (A3) holds for all time and thus $\dot{\rho}_N = 0$ $\forall t$, regardless of whether other variables have attained their steady state values. The final thing to prove for part (*ii*) is that ρ_N^* is an attractor. The sign of $\dot{\rho}_N / \rho_N$ depends on the sign of the LHS of (A3). Since $\xi(\rho_N)$ is monotonically increasing in ρ_M, $\dot{\rho}_N / \rho_N < 0$ when $\rho_N > \rho_N^*$, and $\dot{\rho}_N / \rho_N > 0$ when $\rho_N < \rho_N^*$. The equilibrium is stable and (*ii*) holds.

Finally, since condition (A3) also applies to trading Scenario A for humans, an equilibrium value of ρ_M, denoted ρ_M^A, equals ρ_N^*. However, the fact that Neanderthals may

achieve ρ_N^* does not imply that humans can achieve ρ_M^A. The value ρ_M^A which solves (A3) may

lie anywhere within the unit interval. As ρ_M increases towards ρ_M^A, skilled hunters become less

scarce and the trading scenario might change to Scenario B or Scenario C before ρ_M^A is achieved.

Under Scenarios B or C, condition (A3) is no longer the relevant condition for determining the

equilibrium value of ρ_M.

Proposition 3. An equilibrium value of ρ_M exists for only one trading scenario, and this

equilibrium is globally stable. Moreover, for trading scenarios B and C, the equilibrium value of

ρ_M is less than ρ_N^*.

Proof. Denote the equilibrium value of ρ_M under trading scenario y ($y=A, B, C$) by ρ_M^y. Note

ρ_M may be in an equilibrium (steady state), while other state variables are not. The proof

proceeds in three steps: (i) show that ρ_M^y is unique and locally stable within trading Scenario y,

provided ρ_M^y exists (i.e., $\rho_M = \rho_M^y$ while trading scenario y is still in effect), (ii) show the

existence of an equilibrium under one trading scenario rules out an equilibrium for ρ_M in all

other scenarios, and (iii) show a unique equilibrium value of ρ_M must exist for one trading

scenario and this value is globally stable.

    (i). Suppose ρ_M^A exists within the context of Scenario A. In the proof to Proposition 2, we

showed this value is unique and locally stable. Suppose ρ_M^B exists within the context of

Scenario B. The rate of natural selection in Scenario B is given by equation (13). From (13), an

equilibrium occurs when either $\rho_M = 1$ or when the following condition holds

(A4) $\quad [\eta_{Ms} q_s - \eta_{Mu} q_s \frac{\rho_M}{1-\rho_M} \frac{1-\beta_M}{\beta_M}] - [(1-\eta_{Ms}) q_s \frac{\rho_M}{1-\rho_M} - (1-\eta_{Mu}) q_s \frac{1-\beta_M}{\beta_M}] = 0$

Since $\rho_M = 1$ is impossible when $\eta_{Mj} < 1$ ($j=s,u$), an equilibrium can only occur when condition

(A4) is satisfied. Solving (A4), we find

(A5) $\quad \rho_M^B = \beta \eta_{Ms} + (1-\eta_{Mu})(1-\beta) = 1 - (1-\eta_{Ms})\beta - (1-\beta)\eta_{Mu} < 1$

The proof of local stability is similar to the proof presented for Proposition 2 – it relies on the

fact that the derivative of the LHS of (A4) with respect to ρ_M is negative, as is the case with the

LHS of (A3). To conserve space, we do not present a formal proof here, although we stress that

once $\rho_M = \rho_M^B$ so that (A4) is satisfied, condition (A4) remains satisfied and thus $\dot{\rho}_M = 0 \ \forall t$ regardless of whether other variables have achieved their steady state values. An analogous proof can also be developed to show that ρ_M^C is unique and locally stable.

(ii) From Table 2 (Required Conditions column), it is straightforward to see that Scenario A arises for the smallest values of ρ_M, and as ρ_M is increased the trading system changes first to Scenario B and then to Scenario C for sufficiently large values of ρ_M. The only way an equilibrium value of ρ_M can emerge under multiple scenarios is for the equilibrium value of ρ_M in Scenario A to be less than the equilibrium value of ρ_M arising in Scenario B, which in turn would have to be less than the equilibrium value of ρ_M arising in Scenario C i.e., $\rho_M^A < \rho_M^B < \rho_M^C$ (given fixed q_{Ms}, q_{Mu}, and β_M). Consider the possibility an equilibrium could exist in both Scenarios A and B, in which it must be $\rho_M^A < \rho_M^B$. We now determine if this condition can be satisfied. From Table 2 (Required Conditions for Scenario B), we have

(A6) $\qquad q_{Ms} \dfrac{\rho_M}{1-\rho_M} \dfrac{1-\beta}{\beta} = q_{Mu} + \tau$

where $\tau > 0$. Using (A6), (A4) and (A3) along with the definitions for χ and $\xi(\rho_M)$ from Proposition 2, we have the following condition

(A7) $\qquad \chi - \tau(\eta_{Mu} - (1-\eta_{Mu})(1-\rho_M^B)/\rho_M^B) = \xi(\rho_M^B) < \chi = \xi(\rho_M^A)$

where the inequality holds from (A5). Because ξ is a strictly increasing function, inequality (A7) implies that $\rho_M^A > \rho_M^B$ (and $\rho_N^* > \rho_M^B$) – a contradiction. The existence of an equilibrium in Scenario B implies no equilibrium in Scenario A, and vice versa. An almost identical proof shows that the existence of an equilibrium in Scenario C implies no equilibrium in Scenario A, and vice versa (and also that $\rho_N^* > \rho_M^C$).

Now consider Scenarios B and C, and suppose that an equilibrium exists under each scenario. The existence of an equilibrium in Scenario B requires that $\rho_M^B < \beta$. Using condition (A5), this requirement is written as

(A8) $\qquad \dfrac{\beta}{1-\beta} > \dfrac{1-\eta_{Mu}}{1-\eta_{Ms}}$

For an equilibrium to occur under Scenario C, the following condition, which is analogous to (A4), must hold

(A9) $\qquad \eta_{Ms} - \eta_{Mu} = (1-\eta_{Ms})\dfrac{\rho_M^C}{1-\rho_M^C} - (1-\eta_{Mu})\dfrac{1-\rho_M^C}{\rho_M^C}$

Since $\rho_M^C > \beta$ and hence $\rho_M^C/(1-\rho_M^C) > \beta/(1-\beta)$, we can use condition (A8) and (A9) to obtain the following condition which must be satisfied

(A10) $\qquad \eta_{Ms} - \eta_{Mu} > (1-\eta_{Ms})\dfrac{1-\eta_{Mu}}{1-\eta_{Ms}} + (1-\eta_{Mu})\dfrac{1-\rho_M}{\rho_M}$

Simplifying (A10), we find that this inequality reduces to the condition

$\rho_M^C/(1-\rho_M^C) < (1-\eta_{Mu})/(1-\eta_{Ms}) < \beta/(1-\beta)$, which is a contradiction. The existence of an equilibrium in Scenario B implies no equilibrium in Scenario C, and vice versa.

(iii). If an equilibrium value of ρ_M does not exist under a particular trading scenario, then by the discussion above we know that ρ_M must monotonically increase or decrease until another trading scenario emerges or until $\rho_M = 1$ or $\rho_M = 0$. But $\rho_M = 1$ and $\rho_M = 0$ are not equilibrium options. There must be an interior equilibrium for one of the scenarios, and only one since the existence of multiple equilibria is ruled out by part (ii) of this proof. Moreover, because that equilibrium is locally stable and because it is also approached from other trading scenarios, the equilibrium must be globally stable.

Lemma 1. If ρ_M is initially less than its equilibrium value, ρ_M will attain its equilibrium value even if humans are going extinct.

Proof. Propositions 2 and 3 showed that $\dot{\rho}_M/\rho_M = (1-\rho_M)(\dot{M}_s/M_s - \dot{M}_u/M_u) > 0$ whenever ρ_M is less than its equilibrium value. If humans go extinct without ρ_M achieving its equilibrium value, then $\dot{M}_s < 0, \dot{M}_u < 0$ and $(-\dot{M}_s/M_s) < (-\dot{M}_u/M_u)$. This condition requires that $M_u \to 0$ faster than M_s, and so $\dot{\rho}_M/\rho_M \to \infty$. Since $\rho_M < 1$, the equilibrium value of ρ_M will be achieved before extinction occurs.

Proposition 4. (i) Competitive exclusion of Neanderthals results when humans trade and Neanderthals do not, provided that all biological parameters are the same among humans and

Neanderthals of the same skill class and that humans do not get stuck in trading-scenario A. If humans are trapped in trading-scenario A (or no-trading), co-existence results when there are no biological differences. (ii) However, small differences in one or more of the biological parameters leads to the extinction of the less-accomplished predator species when neither species trades (or when humans are trapped in trading-scenario A).

Proof. (i) A species' sub-population cannot go extinct without the entire species going extinct due to the fertility linkages between sub-populations. We can examine behavioral exclusion by focusing on growth of the total population of each species, removing subscripts for biological parameters since they are assumed identical across species. Proportional growth of the total human population is given by

(A11) $\dot{M}/M = \rho_M \dot{M}_s / M_s + (1 - \rho_M)\dot{M}_u / M_u$

Similarly, aggregate growth of Neanderthals is given by

(A12) $\dfrac{\dot{N}}{N} = (\rho_M + \delta)\dfrac{\dot{N}_s}{N_s} + (1 - \rho_M - \delta)\dfrac{\dot{N}_u}{N_u} = \rho_M \dfrac{\dot{N}_s}{N_s} + (1 - \rho_M)\dfrac{\dot{N}_u}{N_u} + \delta(\dfrac{\dot{N}_s}{N_s} - \dfrac{\dot{N}_u}{N_u})$

where $\delta = \rho_N - \rho_M$.   Assuming $\rho_N = \rho_N^*$ prior   to   human   arrival,   then $\dot{\rho}_N / \rho_N = (1 - \rho_N)(\dot{N}_s / N_s - \dot{N}_u / N_u) = 0$, and so the final term on the RHS of (A12) vanishes and $\dot{N}/N = \dot{N}_s / N_s$.

The equilibrium value of ρ_M will be achieved even if Neanderthals are initially excluding humans by Lemma 1; by Propositions 2 and 3 the equilibrium will be achieved if the human population is growing. Assuming an equilibrium value of ρ_M is achieved, then $\dot{M}_s / M_s = \dot{M}_u / M_u$. Using this relation and subtracting (A12) from (A11), we have

(A13) $\dfrac{\dot{M}}{M} - \dfrac{\dot{N}}{N} = \dfrac{\dot{M}_s}{M_s} - \dfrac{\dot{N}_s}{N_s} = b(1 - \eta_u)(\dfrac{1 - \rho_M^y}{\rho_M^y} m_{Mu}^* - \dfrac{1 - \rho_N^*}{\rho_N^*} m_{Nu}^*)$ $y = $ A, B, C

The expression in (A13) is strictly positive for $y = $ B, C since $m_{Mu}^* > m_{Nu}^*$ under these scenarios (see Table 2) and $\rho_M^y < \rho_N^*$ for $y = $ B, C by Proposition 3. From (A11) and (A12), we can write (A13) more generally as

(A14) $\dfrac{\dot{M}}{M} - \dfrac{\dot{N}}{N} = b[m_M^* - m_N^*]$

where m_M^* is average household meat production by humans and m_N^* is average household meat production by Neanderthals. Conditions (A13) and (A14) therefore indicate that if humans trade according to Scenarios B or C that eventually their per capita meat consumption will exceed that of Neanderthals. Assuming humans achieve trading Scenarios B or C, the proof of Neanderthal extinction follows Proposition 1.

Finally, if humans do get stuck in scenario A, (A14) is satisfied as an equality. Per capita meat consumption is eventually identical among the species and co-existence ensues.

(ii) Suppose neither species trades (Section II). If $q_{Mj} > q_{Nj}$ (j=s,u), with all other biological parameters equivalent between the two species, then $m_{Mu}^* > m_{Nu}^*$. If it is also true that $\rho_M^* \le \rho_N^*$, then equation (A13) is positive and it follows from part (i) that Neanderthals are excluded. If $\rho_M^* > \rho_N^*$ and $q_{Mj} > q_{Nj}$ (j=s,u), *ceteris paribus,* then a greater proportion of the human population is skilled, with both skilled and unskilled humans consuming more meat. The result is greater per capita meat consumption by humans and equation (A14) is positive. Again, it follows from part (i) that Neanderthals are excluded. Finally, if $S_N > S_M$, with all other biological parameters equivalent between the two species, then from equation (9) it is easily shown that $\rho_M^* = \rho_N^*$ and per capita meat consumption is the same. Equations (A13) and (A14) are not valid in this case though, since they are developed assuming $b_N = b_M$. Rather, case 2 of Proposition 1 applies (although with m_i^* equal to average household meat consumption for species *i* as opposed to individual meat consumption).

Appendix II: Parameters for the simulation model.

We have tried to choose parameter values to make the model as realistic as possible. While there is obviously no good data from 30,000 to 40,000 years ago, this is not a concern for our qualitative results. Our results emerge for any reasonable parameter set in which the types of differences between human and Neanderthal parameter values are qualitatively similar to the choices in this paper.

Modeling wildlife (megafauna): The carrying capacity for megafauna is based on evidence on contemporary African megafauna. Mosimann and Martin, studying megafauna hunting in North America, use a megafauna density of 25 animal units (AU) per square mile which. Assuming an available range of 3 million square miles, this translates into k=75 million AU. 1 AU measures 1,000 pounds of living animal. Assume the intrinsic growth rate of megafauna is 15%; a number somewhat lower than the optimistic number (25%) reported by Mosimann and Martin for mammoths, but higher than estimates of the growth rate of modern elephants (close to 7%).

Modeling human and Neanderthal population and behavior: We assume an initial population of 100 households. The mortality rate is d =0.08. Over the past 200 years, U.S. mortality rates have fallen from about 0.04 to less than 0.01. We therefore view our chosen value for approximately 30,000 - 40,000 years ago to be somewhat conservative. We assume a prehistoric working day for the representative household (man, woman and two kids) consists of about 20 hours per day (7300 hours per year), and that meat is the predominant source of food so that β=0.6. Finally, Dasgupta (1993) estimates that active humans should consume 2000 calories per day (0.73 AU/year) to sustain themselves, thus S=2.9 AU/year for our representative household.

Modeling harvesting of megafauna: Mosimann and Martin assume that a single full-time hunter supports an entire family and harvests 13 AU per year for a wildlife density of 25 AU per square mile (i.e., x=75 million). Assuming the standard Schaefer production function $y=qex$, and that a full-time hunter goes out for 10 hours a day, we find that $q = 4.7\times10^{-11}$. Next, according to Mosimann and Martin, if megafauna density falls to 5 AU per square mile (so that x=15 million), it is assumed that the annual harvest is reduced to 6.5 AU. Again, solving for the catchability coefficient we find that $q = 1.2\times10^{-10}$. As a benchmark parameter in our simulations, we apply the average of these two parameters, or $q = 8.3\times10^{-11}$.

Table 1. The principle of biological exclusion

Scenarios in which humans are more biologically efficient	Time from introduction of humans to Neanderthal extinction (years)
$q_{Mj}=1.03q_{Nj}$ $(j=s,u)$	8,861
$l_M=1.03l_N$	8,861
$\beta_M=1.03\beta_N$	8,861
$S_M=0.97S_N$	8,828

Note: In each scenario, all parameters are the same among humans and Neanderthals of like skill classes, with the exception of the parameters indicated.

Table 2. Trading equilibria

Trading scenario	Required conditions	Consumption by skilled hunters		Consumption by unskilled hunters	
		Meat (m_{Ms}^*)	Other goods (v_{Ms}^*)	Meat (m_{Mu}^*)	Other goods (v_{Mu}^*)
A. Skilled hunters hunt; unskilled hunters hunt and produce other goods	$\beta_M > \rho_M$, $\quad q_{Ms}/q_{Mu} < ((1-\rho_M)/\rho_M)\beta_M/(1-\beta_M)$	$\beta_M q_{Ms} l_M x$	$(1-\beta_M)(q_{Ms}/q_{Mu})l_M$	$\beta_M q_{Mu} l_M x$	$(1-\beta_M)l_M$
B. Complete division of labor: skilled hunters hunt; unskilled hunters produce other goods	$\beta_M > \rho_M$, $\quad q_{Ms}/q_{Mu} > ((1-\rho_M)/\rho_M)\beta_M/(1-\beta_M)$	$\beta_M q_{Ms} l_M x$	$\beta_M l_M (1-\rho_M)/\rho_M$	$(1-\beta_M)l_M q_{Ms} x \rho_M/(1-\rho_M)$	$(1-\beta_M)l_M$
C. Skilled hunters hunt and produce other goods; unskilled hunters only produce other goods	$\beta_M \le \rho_M$	$\beta_M q_{Ms} l_M x$	$(1-\beta_M)l_M$	$\beta_M q_{Ms} l_M x$	$(1-\beta_M)l_M$

Note: These equilibria are not steady states. Instead, they are the solutions to the static market equilibrium problems faced by humans at each point in time.

Table 3. A principle of behavioral exclusion: no biological differences

Fertility scenarios	Time from human arrival to Neanderthal extinction	Equilibrium trading scenario	Equilibrium ρ_M	Equilibrium ρ_N
1. $\eta_{Ms} = 0.8$ $\eta_{Mu} = 0.8$	7,464	B	0.56	0.60
2. $\eta_{Ms} = 0.8$ $\eta_{Mu} = 0.6$	3,518	C	0.67	0.70
3. $\eta_{Ms} = 0.6$ $\eta_{Mu} = 0.8$	Co-existence	A	0.38	0.38

Table 4. Behavioral exclusion when Neanderthals are more biologically efficient

Fertility scenarios	Parameters for which Neanderthals are more efficient				
	q_{Ns}, q_{Nu}	l_N	S_N	η_{Ns}	η_{Nu}
1. $\eta_{Ms} = 0.8$ $\eta_{Mu} = 0.8$	Human extinction (0.03)	Human extinction (0.03)	Human extinction (0.03)	14,412 (0.09)	9,427 (0.32)
2. $\eta_{Ms} = 0.8$ $\eta_{Mu} = 0.6$	9,570 (0.07)	9,451 (0.07)	10,530 (0.07)	4,236 (0.24)	3,653 (1.0)

Note: Table entries represent the time (in years) from human arrival to Neanderthal extinction when parameter ω is more efficient by ψ=0.05, i.e., $\omega_N = (1+\psi)\omega_M$ for ω = q, l, and η_s and $\omega_N = (1-\psi)\omega_M$ for ω = S and η_u.

Numbers in parentheses indicate the maximum value of ψ such that Neanderthal extinction occurs.

Table 5. Comparative statics: results under alternative parameter specifications

Alternative scenarios	Time from human arrival to Neanderthal extinction	Equilibrium trading scenario	Equilibrium ρ_M	Equilibrium ρ_N
1. k is reduced by 50%	7,368	B	0.56	0.60
2. r is reduced by 50%	6,988	B	0.56	0.6
3. Comparative advantage ratio q_s / q_u is increased by 50%	2,797	B	0.56	0.73
4a. The elasticity of substitution (σ) is decreased by 20%	30,020	A	0.6	0.6
4b. The elasticity of substitution (σ) is increased by 20%.	2,464	C	0.5	0.61
5a. Congestion externalities ($r=0.001$, $z_{MN}= z_{NM} =0.05$)	7,628	B	0.56	0.60
5b. Congestion externalities ($r=0.005$, $z_{MN}= z_{NM} =0.05$)	9,318	B	0.56	0.60
5c. Congestion externalities ($r=0.001$, $z_{MN}= z_{NM} =0.9$)	7,549	B	0.56	0.60

Note: For each scenario, all parameters values are as defined in fertility scenario 1 in Table 3, except for those

differences mentioned here under the column heading "Alternative scenarios".

Population

400000

Neanderthals

Humans

300000

200000
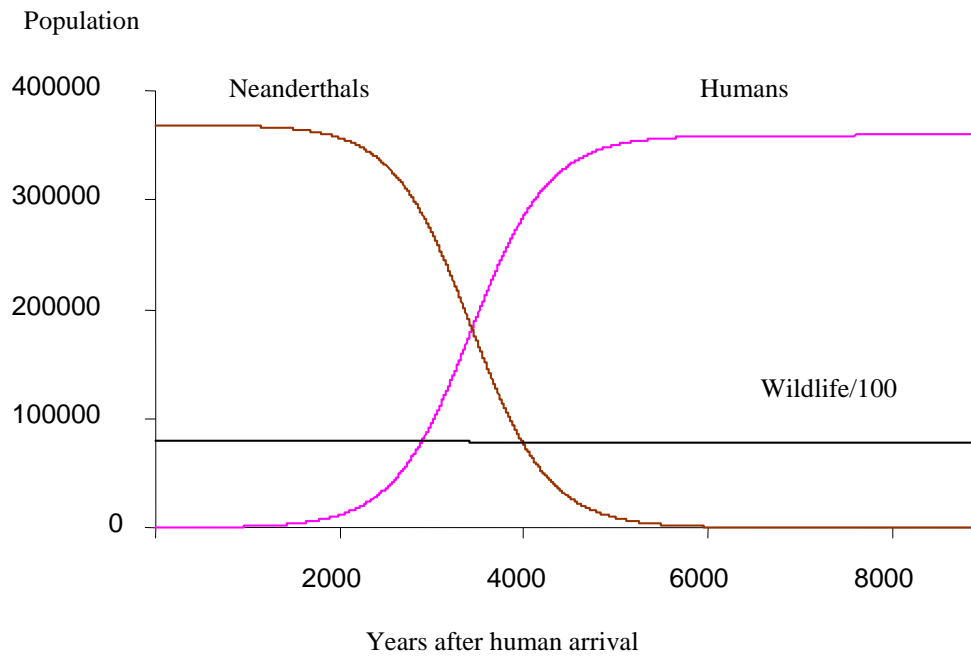
Wildlife/100

100000

0

2000   4000   6000   8000

Years after human arrival

Figure 1. Competitive Biological Exclusion