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Coevolutionary History

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Coevolutionary History

Coevolution (the process in which populations of two species shape each other over time) has been one of the most important processes in history. It has also been one the least appreciated. Its low profile grows partly out of the disciplinary divide between human history and natural science, partly out of historians' reliance on sources that did not recognize it, and partly out of the ease with which one can take its products for granted. But look at some of its effects. By ushering in the Agricultural Revolution, it was responsible for the transition from prehistory to history (traditionally defined). It was the primary means of increasing physical power for almost all of history. It helped spark, and sustained, the Industrial Revolution. It helped human numbers to soar from 954 million to 7.1 billion in the past two hundred years. It was responsible for the food people ate, the way they made their living, the diseases they suffered, and the technology they developed. Not a trivial list of accomplishments.[1]

Elsewhere, I have encouraged historians and evolutionary biologists to join forces in a research program known as *evolutionary history*.[2] This essay aims to encourage historians to study *co*evolution as a historical process, which in turn can lead to new interpretations of well-studied events. Because common concepts about evolution can block our ability to see coevolution, the first section of the essay will clarify the meaning and mechanisms of evolution and coevolution. The second section examines the role of coevolution in creating and sustaining the Agricultural Revolution. The third section explains why coevolution was one of the most important processes for increasing human power. The fourth section discusses ways in which coevolution helped to usher in and support the Industrial Revolution.

Coevolution is the process in which populations of different species evolve repeatedly in response to each other. The key ideas are reciprocity and continual change. Population A leads population B to evolve, the new version of population B leads population A to evolve, the new version of population A leads population B to evolve again, and so on through time. The idea of coevolution was first developed to explain why flowers seemed perfectly designed for the specific species of insects that pollinated them. Most likely, the traits of populations of plants, and traits of populations of their insect pollinators, changed repeatedly in response to each other. Other examples of coevolution include fleet predators and prey (when one became faster, the other had to become faster, too, to survive) and the development of leguminous plants with nitrogen-fixing bacteria that inhabit their roots.[3] Coevolution may involve populations of three or more species, but, for simplicity's sake, this essay focuses on pairs of populations.

Historians would have nothing to study without coevolution because human beings probably would not exist. We might think of our bodies as entirely human, but it would be more accurate to think of them as porous ecosystems swarming with bacteria, fungi, protozoa, and viruses. Symbionts in our guts, hair, skin, and mouths help us survive by digesting food and protecting us from disease. They make up 90% of the cells in our bodies. Human cells are larger than bacterial and fungal cells, so our bodies are more human that not when it comes to volume, but our bodies are more bacterial than human when it comes to numbers. We have a lot to learn about human microbiota, the extent of which has only recently been documented, but evidence suggests that coevolution has adapted us to our microbiota and vice versa.[4] (Please see Julia Thomas's essay in this issue for more on this topic.)

Coevolution in history occurred when populations of people and of non-human species repeatedly shaped each other's traits over time. The idea that people can prompt evolution is unfamiliar to many scholars outside biology, so let me clarify the meaning of evolution before returning to coevolution. A popular definition equates evolution with the development of new species over millions of years through natural selection. If accurate, this definition would disqualify people as evolutionary actors. Few of us can identify a species that people created. Our species could not affect other species over millions of years because *Homo sapiens* developed perhaps 195,000 years ago. If *nature* refers to the non-human world, then natural selection would seem to exclude human actions. The problem with the popular definition is that it is too narrow. All development of new species over millions of years through natural selection is evolution, but not all evolution is development of new species over millions of years through natural selection.[5]

Biologists, on whose concepts we will rely in this essay, define *evolution* as change in the frequency of inherited traits in populations over generations. This definition contrasts with the popular definition in at least six ways. First, the entities that evolve are populations, not necessarily entire species. Populations consist of members of a species that live in a given place and usually do not interbreed with members of other populations. Sometimes all populations of a species evolve, in which case the species evolves, but local populations can evolve without affecting other populations of the same species. Second, any degree of change qualifies as evolution. Sometimes changes are so radical that populations become new species, but most evolution involves smaller changes within populations. All changes in the frequency of inherited traits of populations over generations are evolution, even if temporary and later reversed. Third, the time required for evolution is only two generations, not a specific or large number of years. Species with short generation times, such as bacteria, can evolve in hours. Fourth, natural selection and evolution are different processes. *Natural selection* is a mechanism that leads to evolution. It is the differential survival of *individuals* due to differences in traits. Selection acts *within* generations. *Evolution* means change in frequency of inherited traits in *populations*. It happens *across* generations. Fifth, evolution does not require natural selection. I will describe other evolutionary mechanisms below. Sixth, evolution is defined by a pattern (change in inherited traits), not by the cause of the pattern. People are as eligible as any other species to affect evolution.[6]

An example from Africa shows how evolution can take place in historical time as a result of human action. In some populations of elephants, the frequency of an inherited trait (tusklessness) increased over the twentieth century. Two mechanisms other than natural selection (if taken to exclude human actions) were responsible. One was human selection. Poachers killed elephants for their tusks, which they sold into an international ivory market. Poachers had no reason to kill tuskless individuals, which survived and reproduced at a higher rate than tusked individuals. Another mechanism probably was *drift*, which means differences in reproduction rates of individuals due to chance. Once elephant populations became small, tuskless individuals apparently reproduced more often than tusked individuals by chance, which led tusklessness to increase even in the absence of poaching.[7]

In addition to situating evolution in (not outside of) history, this example illustrates the need for historians and biologists to join forces to understand the way life has changed over time. The traditional tools of historians do an excellent job of explaining the social factors that led to selection for tusklnessness. Art historians can explain the development and appeal of ivory carving, economic historians can analyze the development of the international ivory trade, political historians can explain why some African countries lacked the capacity or desire to enforce laws against elephant hunting, and social and economic historians can analyze the enduring poverty that created a strong incentive for poaching. But the traditional tools of history cannot explain why killing tusked elephants encouraged tusklessness over generations. The tools of biology can. Genetics explains how elephants inherited tusklessness from their parents. Evolutionary biology explains why tusks evolved (they aided survival and reproduction) and why they became less common (hunting made the risks of tusk-bearing outweigh the benefits). Reducing populations to a few individuals increased the odds that chance differences in reproduction would affect the frequency of traits in populations.

Another example of evolution in history illustrates the life and death consequences of coevolution. The earth sustains more than seven billion people today only because of coevolution that resulted in highly productive, domestic plants and animals and people who knew how to tend them. But coevolution also has sent millions to their graves. The end of one of the earth's great killers, malaria, hove into sight after World War II when new insecticides (to kill malaria-carrying mosquitoes) and drugs (to kill malaria plasmodia) became common. The worldwide malaria eradication project made stunning progress until mosquitoes and plasmodia evolved resistance to insecticides and drugs. The end of malaria receded back over the horizon, and the World Health Organization abandoned the eradication project. By 2000, about 2 million people died yearly of malaria, and the disease infected 300-500 million more. Between these poles of life and death lie thousands of other examples of coevolution that changed the lives of human beings, and the lives of members of non-human species, in ways large and small.[8]

Human beings have affected the evolution of populations of other species through many mechanisms. Charles Darwin named two of them. *Unconscious selection* is the process in which people affect the traits of populations without intending to do so, usually by helping individuals with certain traits survive more often than those with other traits. (Unconscious selection by people served as Darwin's model for natural selection in the wild.) Selecting for tusklessness is an example. *Methodical selection* is the process in which people affect the traits of populations intentionally through selective mating or by limiting reproduction to favored individuals. Plant and animal breeding are examples. We have already mentioned a third mechanism, *drift* (the change in frequency of traits in a population due to chance differences in reproduction of individuals with those traits). Recently, a fourth means, *genetic engineering*, has provided a powerful way to modify the traits of populations, including by moving genes from one kingdom to another. (Genetic engineering might be considered a form of methodical selection, but its microbiological techniques differ from traditional breeding.) Frogs, tobacco plants, and monkeys now glow in the dark or under ultraviolet light thanks to genes from fireflies and jellyfish, and tobacco and lettuce plants manufacture insulin thanks to the insertion of a human gene. The pervasive impact of human beings on evolution has led an evolutionary biologist to suggest that we are living amidst an anthropogenic "evolution explosion."[9]

Anthropogenic evolution led to coevolution when changes in traits of non-human populations circled back to change traits of human populations. A dramatic recent example is the coevolution of human populations with genetically engineered organisms that manufacture medicines. The U. S. Food and Drug Administration first approved the use of a product of genetic engineering, insulin from genetically modified bacteria, in the early 1980s. Genetic engineers had changed a trait of a bacterial population, and this new trait in a bacterial population circled back to change the frequency of a trait, symptoms of diabetes, in a human population. The same can be said about symptoms of other human diseases that have declined due to coevolution with genetically engineered, non-human populations. By 2009, the U. S. Food and Drug Administration and the European Medicines Agency had approved the use of 151 products of genetic engineering. Forty-five of them came from populations of a single species of bacteria, *Escherichia coli,* so human populations were coevolving with at least 45 genetically distinct populations of *E. coli*. Other products have come from genetically modified populations of yeast, an insect, and mammals.[10]

Historians have long recognized that the Agricultural Revolution was the most important revolution in history. The development of agriculture led to settled populations, large social groups (towns, cities, states, empires), hierarchical social structures, occupational specialists outside agriculture (including the scribes who invented writing), growing populations, increased crowd disease (picked up from domestic animals), and conquest of hunter gatherers by farmers. The Agricultural Revolution laid the foundation for nearly everything historians have studied, and historians traditionally have used one of the revolution's byproducts (the invention of writing) to mark the end of prehistory and the beginning of history.[11]

Historians (and other scholars) have credited the Agricultural Revolution to domestication, making it one of the most important processes in history. Most definitions of *domesticate* resemble Webster's: "to adapt (an animal or plant) to life in intimate association with and to the advantage of humans." This definition has several key features, most of them implicit. First, domestication is an evolutionary process (adaptation). Domestication requires changes in traits of populations to suit them to a human environment. Second, domestication changes non-human organisms. The definition does not preclude human change, but neither does it require it. Third, the benefits of domestication flow to people. The definition does not preclude benefits to non-human organisms, but neither does it require it. Fourth, domestication might be a one-time event. The definition does not preclude continual change after domestication, but neither does it require it. Fifth, the emphasis on one-way impacts makes it is easy to assume that people initiated the process. Explicitly or implicitly, historians have used *domesticate* and *domestication* in ways consistent with these meanings. Studies often describe domestication as a one-way, and implicitly one-time, process that people initiated and controlled thousands of years ago.[12]

Coevolution offers a better way of thinking about domestication and history. Crediting the Agricultural Revolution to domestication, as usually understood, is partly correct. People did change the traits of plant and animal populations in ways that enabled them to live with, and benefit, human beings thousands of years ago. This process was necessary for the Agricultural Revolution, but it was not sufficient. The traits of human populations also had to change during domestication, making the process bidirectional. It is probably more accurate to think of domestication as a relationship between populations of two species, rather than as a state into which one puts the other. As Bruce Smith put it, "The establishment of such a new and sustained pattern of interaction…is clearly the independent variable or component in the causal chain—the behavioral relationship *is* domestication." For agriculture to thrive and spread, human and non-human populations had to continue to coevolve right up to the present. The process has not been glamorous or well recognized, but it has been essential.[13]

Domestication always required coevolution. That is, human populations had to develop certain traits for the process to succeed. The most obvious traits were behavioral, such as saving and planting seeds. Many authors have attributed domestication to methodical selection (usually using other terms, such as breeding or selective mating). This interpretation accords with a common sensibility that historical change results from human intentionality. Methodical selection might have played a role in the first domestications, but it seems unlikely. Human beings lived as hunter-gatherers for most of history (broadly defined to include the hunter-gather era), and it is hard to imagine why people would decide to domesticate plants and animals without evidence such efforts would be necessary or successful. The traditional argument is that population growth forced people to adopt agriculture. This explanation is plausible, but we should not make Malthus's mistake of assuming human populations grew without check.

Hunter-gatherers adapted their population size (through abstinence, abortifacients, and infanticide, for example) to their food supply.[14]

Unconscious selection seems likely to have played an important, even primary, role. People acting for short-term gain could have, in the long run, modified the traits of non-human and human populations enough to result in domestication. One of the best tests of this hypothesis came in experiments by the Russian geneticist Dmitry K. Belyaev. He domesticated foxes by selecting only for one trait, tameness, which he defined as willingness to approach human beings. After twenty generations, 35% of the foxes showed behaviors we associate with dogs. They ran to people, licked their faces, responded to pet names, and wagged their tails. It is easy to imagine that people and wolves domesticated each other by a similar process. Wolves willing to approach hunter-gatherer camps may have scavenged more food than their skittish relatives, giving them an advantage in survival and reproduction, which eventually might have led to domestic wolf populations (aka dogs). One of the unexpected findings from Belyaev's experiments was that selection for tameness could also produce physical traits seen in domestic animals. Many tame foxes had traits found in dogs, such as black and white fur and droopy ears. If we need further proof that domestication could develop unconsciously, we need only look to the animal world. Ants have coevolved domestic relationships with fungi and insects (aphids and other species of ants), and no one has credited them with advanced cognition.[15]

A coevolutionary approach addresses another flaw in the traditional definition of domestication: the assumption that people initiated the process. We could just as easily assume that non-human populations initiated the process. Take the example of wolf domestication via camp followers. Certain wolf behaviors could have elicited and rewarded certain human behaviors. Wolves near human camps could have warned of approaching enemies (human and animal) and transported fresh meat (their own muscles) to new campsites, where people could slaughter them as needed. These behaviors could have encouraged human groups to keep wolves nearby by feeding them waste or surplus food. We can say similar things about plants. Yes, people probably helped maize develop from teosinte by selectively harvesting unusually large heads. But it would be equally accurate to say that teosinte began the process by producing unusually large heads, which encouraged human beings to selectively harvest and plant them. Rather than forcing us to choose one partner or the other as initiator, as the common understanding of *domestication* does, coevolution enables us to focus on the actions of both partners in evolving a relationship.

A coevolutionary framework also corrects the assumption that only people benefited. People did, but so could partner populations. The two populations were mutualists (partners in a symbiotic relationship in which both benefited). One way to measure benefit is to look at reproductive success. Which sub-species of wolves has more offspring in North America today—wild wolves (*Canis lupus lupus*) or domestic wolves (*Canis lupus familiaris*, aka dogs)? The answer is dogs, by a long shot. Human beings devote billions of dollars and countless hours to succoring dogs (and other domesticates). Domestic organisms suffer some costs under domestication, such as being slaughtered, but people also incur costs from the relationship (such as catching epidemic diseases). So the two populations were parasites (partners in a symbiotic relationship in which both suffered costs) as well as mutualists.[16]

I have been describing changes in the frequency of behaviors in human populations as evolution (that is, change in frequency of inherited traits), which might be surprising. Many of us are accustomed to thinking of traits as physical features. But behaviors are traits of individuals and populations, too, and they can be just as essential for survival and reproduction (think of feeding and mating). Even if we recognize behaviors as traits, it might be hard to see how they could evolve because evolution requires inheritance of traits. We know that genes provide a means of inheriting physical traits. Are behavioral traits also genetic? Some behaviors, such as beating of hearts and breathing, are largely under the control of genes (though we can consciously affect both if we wish). Other behaviors have no clear genetic basis (beyond creating the ability to perform the behavior). We can cheer for a new football team when we move to a new city, but genes cannot explain the new behavior. Genes stay the same throughout one's lifetime.

The answer to this conundrum lies in recognizing that many species, including people, have at least two means of inheritance: genes and culture. Scholars have used *culture* to mean many things. In this essay, I follow the lead of anthropologists and other scholars and use it to mean ideas about how to do things. *Instructions, recipes, practices, rules*, *traditions*, *customs,* and *guidelines* mean roughly the same thing. They all refer to instructions for behaviors (or instructions for interpreting the meaning of the behaviors of others, including their words). The key point is that culture and genes both transmit instructions for traits (physical or behavioral), so behaviors grounded in culture (or in genes) can evolve. Cultural inheritance resembles genetic inheritance in several ways. It carries instructions for traits from parents to offspring. Instructions for a trait may come in multiple versions (alleles). Some traits might result from a single instruction, but others result from the combination of multiple instructions. Instructions might be copied faithfully, or copying may introduce changes. Culture also differs from genes. Culture passes among non-relatives, and backward in generations (from offspring to parents). Culture is learned, so it can change multiple times within an individual's lifetime, rather than staying the same, which enables cultural traits to evolve more rapidly than genetic traits. (This learning may be conscious, as in schooling, or it may be unconscious, as when we accidentally memorize an advertising jingle.) Culture can be stored outside bodies (e.g., in a book), as well as in bodies (brains).[17]

Now we can see that human and non-human populations coevolved during and after the Agricultural Revolution by dancing to four styles of music. First, and probably most commonly, human populations changed culturally and non-human populations changed genetically. Many wild plants bear seeds on delicate stalks that shatter when touched, which can make it hard to gather seeds, but some individual plants happened to have tough stalks that retained seeds despite handling. People developed the practice of harvesting wheat heads with tough stalks because attached kernels were easier to locate, gather, and transport. This practice selected for tough stalks in wheat populations, so the trait increased in frequency in domestic populations. The strength of stalks is a genetic trait. Tough stalks in wheat selected for preferential harvesting and planting of wheat with this trait by people. Preferential harvesting is a cultural trait.[18]

Second, human and non-human populations both changed genetically. One of the best-known genetic changes in people was the development of lactase persistence (also known as lactose tolerance). Lactase is an enzyme that breaks down lactose, a sugar in milk. Usually mammals stop producing this enzyme after weaning. They retain the gene with instructions for making lactase, but a control region of DNA turns off the gene. Adults with shuttered lactase genes experience gastro-intestinal distress (gas and diarrhea) if they consume dairy products. Such is the experience of most human adults, who are known as lactose intolerant.

In populations with a long history of dairying, however, a high percentage of adults tolerate lactose because their bodies continue to make lactase after weaning. Most likely the ability to digest milk in adulthood offered some advantage in survival and reproduction in the past. The idea that selection, rather than drift, was responsible for the frequency of the trait gains support from the fact that multiple dairying populations evolved the same trait (lactase persistence) independently. Lactase persistence is common in Northern Europeans and in North African populations with a history of raising cattle, but the genetic codes leading to this common trait are different in the two populations. Both codes short circuit the DNA control region that would turn off the lactase gene, but they short it in different spots. Members of populations that evolved lactase persistence carried this trait with them as they migrated elsewhere in the world, such as North America and the Antipodes.[19]

Agriculture appears to have rewarded genetic change in human populations in other ways, too. Individuals from populations that eat a lot of starch have more copies of a gene responsible for an enzyme that breaks down starch (amylase) than do individuals from populations that eat little starch. Agricultural diets appear to have selected for genes that affect metabolism of proteins, carbohydrates, and lipids (fats). Genes that shape the thickness of tooth enamel, the ability to taste bitter foods, and the breakdown of alcohol also appear to have been favored by agricultural diets. Agriculture appears to have favored alleles that conferred immunity to malaria and other crowd diseases. Agriculture increased the frequency of crowd diseases because people lived in close quarters with domestic animals, the incubators of human crowd diseases, and because the diseases spread quickly in dense human populations.[20]

Lactase persistence is probably also a product of a third type of coevolution under agriculture: genetic evolution by people and cultural evolution in non-human populations. We already described genetic evolution in people (lactase persistence). Milk cows did evolve genetically, but milking required that they evolve culturally, too. Genetic makeup may have conferred some placidity, but cows learned to stand still and minimize kicking during milking. Experiments have shown that cows recognize individual human beings and modify their behavior in predictable ways based on past experiences with them. They learned to stand farther away from "aversive" handlers than from gentle handlers, and aversive handling produced less milk than gentle handling.[21]

In a fourth type of coevolution under agriculture, human and non-human populations both evolved culturally. Keepers of domestic animals had to develop certain behaviors to keep their partner populations alive and productive, such as supplying or taking them to food and water. These animals developed certain behaviors that enabled them to take advantage of resources, such as coming to barns in the evening. Sometimes people encouraged behaviors deliberately, a practice we usually call training. At other times people encouraged behaviors accidentally, such as when cows learned to stand away from aversive handlers. Either partner in a coevolved relationship could train the other. I have trained my dog to sit, and he has trained me to open doors for him (he stands in front of a door and barks once when he wants to come inside the house).[22]

Another advantage of a coevolutionary framework for agriculture (the list keeps growing) is its emphasis on continual change. Simply domesticating a non-human population and keeping its traits constant was a recipe for failure. Yields of crops would decline, and mortality of animals would rise. The reason is that domestic plants and animals did not live entirely under human control. They had other, non-human coevolutionary partners, too. Insects, fungi, bacteria, and viruses lived and dined on agricultural animals and plants. Plants and animals evolved defenses against these enemies, such as poisons in plants and immune systems in animals. But the evolution of defenses in one population creates selective pressure in enemy populations. Insects evolved the ability to detoxify certain plant poisons, and the degree of virulence in pathogens changed. Freezing the traits of domestic plant or animal strains made them sitting ducks for the next round of offensive firepower in their enemies, which invited disaster for farmers.[23]

Farmers wanting to avoid losses had several options open to them. The first was to select for resistance to enemies. If a disease devastated a field of crops, and a few individual plants happened to have traits that conferred resistance to the disease, farmers wanting to harvest seeds for the next year had no choice but to use seeds from surviving plants. It did not matter whether the selection for resistance was conscious or unconscious; the benefit would be the same. The second strategy was to introduce new varieties from elsewhere, thereby changing the traits of the local population. Both of these first two strategies involved genetic evolution in agricultural species. The third strategy was for farmers to evolve new cultural traits, including the development and use of technologies. Antibiotics, vaccines, and pesticides are examples of technologies that people developed to insert themselves into the coevolutionary arms race between agricultural populations and their enemies.[24]

Similarly, agriculture depended on coevolution after domestication to increase agricultural yields. The first domestic populations of plants and animals would have been little more productive than their wild relatives. Agricultural productivity rose because farmers selected for individuals with more of what farmers desired, such as simultaneous seed ripening, compact heads of grain, tough stalks, simultaneous seed germination, big kernels of grain, many kernels per head, large fruit, copious meat, fatty meat, and long fiber (plant and animal). The resulting growth in productivity released a higher percentage of human populations to pursue occupations other than farming.[25]

Coevolution after domestication was essential for agriculture to spread. The wild ancestors of domestic plants and animals typically inhabited smaller ranges than their domestic descendants. Bigger geographic ranges meant bigger ranges of environmental conditions, such as temperature, water, soil, fodder, and day length. Survival in new places often required modification of the traits of domestic populations beyond those required for domestication. This happened partly through unconscious selection. If farmers planted seeds in a new place, only individual plants that tolerated new conditions would survive to produce seeds to be planted the next year. Adaptation also has happened through methodical selection. Efforts in the nineteenth and twentieth centuries to expand the range of Sea Island cotton (*Gossypium barbadense*) from coastal areas to the American Southwest, for example, failed repeatedly until breeders developed strains (known as Pima cotton) that tolerated desert conditions.[26]

Power is one of the most important concepts in history. Historians in many fields use the term, often without defining it. This essay will use *physical power* in the sense defined by physicists: the rate at which energy is put to work. Units for measuring power include horsepower and watts. The definition of power guides our attention to two key items: devices that convert energy to work (engines), and the sources of energy. It is important to study physical power not only for its own sake, but also because it has contributed to social power (in this essay, meaning roughly getting other people to do what one wants). Social power might have multiple sources, such as access to knowledge, but nothing social happens without some physical action, at minimum by human bodies. Multiplying one's physical power also has increased social power (as military and political leaders have long known).[27]

Until the mid-20th century (that is, for almost all of history, however defined), most people relied on muscles as the primary devices for converting energy to work. Many people in rural Asia, Africa, and Latin America still do today. Nothing highlights the importance of muscles more than the units of power that pioneers of the Industrial Revolution chose to use: horsepower. The developers of steam engines needed to explain to potential buyers how much work their devices could do, so they measured output in terms of their competition. In their markets, the dominant engines were horses, so steam entrepreneurs defined one horsepower as the weight a horse could lift or pull a certain distance in a certain time. This unit enabled buyers to compare the cost of doing the same work with equine muscles or with steam engines.[28]

Coevolution was responsible for developing both animal engines and the energy sources that fueled them. Coevolution shaped the bodies, temperaments, and culture of animals to make them useful in harness. Workhorses and racehorses both lived in Britain in the 18th century, but strong, heavy, patient workhorses looked and behaved very differently from fleet, lithe, and flighty racehorses. In comparing their engines to horses, steam entrepreneurs were not comparing them to racehorses, but to animal engines designed for the same purpose (lifting or pulling weight). The fuel for animal engines came largely from products of human-plant coevolution, such as oats, including parts of plants unfit for human food. Fuel also could come from wild plants, such as grasses. One of the virtues of animal engines was their ability to use flex fuels (domestic and wild plants). Bullocks in India lived on crop byproducts (rice straw, mustard oil cakes, chopped banana leaves) and on plants growing along roadsides and canals.[29]

Horses (and other draft animals) were not the only muscular engines. The first, and always essential, engines of history were human muscles. People sometimes used their own muscles to do work, and sometimes they persuaded, paid, or forced other people to work for them. (Social and physical power reinforced each other when some people benefited from the work of others.) In all these cases, human muscles were engines that converted food energy to useful work. After the Agricultural Revolution, most of the food energy that fueled human muscles came from domestic plants, especially those that stored energy in carbohydrates (wheat, rice, maize, and potatoes). Some domestic plants supplied muscle fuel in the form of fats (e.g., nuts and seeds). In wealthier societies, fat from domestic animals also fueled human muscles. The energy in animal fat derived from plants, both domestic and wild. Coevolution was responsible for developing the domestic plants that supplied fuel to human muscles both directly (plant food) and indirectly (animal fat). It was also responsible for the domestic animals that turned domestic and wild plants into fat that fueled human muscles.[30]

The coevolution that led to draft animals multiplied human power both directly and indirectly. Animal muscles multiplied human power directly by virtue of numbers (one person could control the work of many animals) and of strength (one ox could haul a bigger block of stone than a person could). It took 100-200 hours for a peasant to prepare a hectare of land for planting using a hoe, and a little over 30 hours to do so with a single ox drawing a plow. Domestic animals multiplied human power indirectly by increasing yields of domestic plants (thus food energy for people and for animals). They did this both with their muscles (e.g., by pulling plows, which helped farmers raise more crops, and by lifting irrigation water from wells) and with their guts (by turning fodder into manure, the primary fertilizer for fields before synthetic fertilizers in the twentieth century). Manure production depended on coevolution of domestic animals with non-human species that, unlike the enemies mentioned above, benefited animals (making them mutualists). Ruminants (cattle, sheep, goats) and horses could not break down cellulose themselves. Billions of microbes (bacteria, protozoa) in their digestive tracts did it for them.[31]

Animal power was crucial not just for agriculture, but for the activities studied by all fields of history. To mention just a few examples, domestic animals lifted, via ropes and pulleys, the stones that built the great cathedrals of Europe (history of art, architecture, and religion), carried goods along the Silk Road (economic history), hauled soldiers and weapons into battle through World War I (military history), and enhanced the mobility of hunters on the Great Plains of North America (Native American and social history).[32]

Coevolution was one of the most, and possibly the most, important means of technological invention and development in history. Artifacts that people use to do human work are tools, and all tools are technologies. Every time human groups coevolved domestic relationships with new populations, they invented new types of tools. And every time they adapted a plant or animal to a particular place or use, they further developed the tool. We easily recognize mechanical invention and development in history, and we readily credit these processes with transforming the world during and after the Industrial Revolution. But many of us are not accustomed to seeing the world-transforming power of biological invention and development.[33]

Saying that coevolution was essential for the Industrial Revolution runs counter to a dominant narrative in which machinery replaced biology as the driving force in history. In fact, coevolution made the Industrial Revolution possible in at least three ways. These contributions were not sufficient for industrialization, but they were necessary.

First, coevolution enabled inventors to work. The nation of the Industrial Revolution's birth, England, was a nation of tinkerers who invented machinery, such as steam engines and cotton spinning machines, which helped transform the world. The mechanics owed their ability to focus on invention and development to farmers who produced more food than they needed themselves. The productivity of farmers derived from their coevolution with domestic plants and animals. This may seem like an obvious point, and it is, but it is a mistake to take the obvious for granted. If we want to explain how automobiles work, we know we need to talk about the role of gasoline in supplying the energy that turns the engine. It would be good to develop a similar habit and consider the role of food in supplying the energy that occupational specialists and social systems need to function.

Second, coevolution supported the Industrial Revolution by powering the bodies of workers. Most of the research on energy in the Industrial Revolution has focused on waterpower (especially in the early years) and the burning of coal, and for good reason. These energy sources fueled the machines essential for industrialization. Often overlooked, however, was an equally essential source of energy, food. All the coal in the world would have been useless without workers to operate the machines that ran on coal. The leaders of the Industrial Revolution recognized this fact. England could not grow enough food to support its workers, so industrialists helped lead the fight to reform the Corn Laws and liberalize grain imports. England turned to imports from the United States (among other places). The productivity of American farmers depended partly on fertile soils and partly on coevolution that adapted European wheat varieties to American conditions, increased yield, and maintained yields despite coevolution with enemies that otherwise would have sent yields plummeting. When pests and pathogens circumvented the defenses of a wheat variety, farmers adapted culturally by substituting another.[34]

Third, coevolution produced cotton with traits suited to mechanization. Most of this essay has focused on the importance of coevolution for food, but it was also important for fiber. Mechanization of cotton textiles has long been considered a leading edge, and paradigmatic example, of the Industrial Revolution. The first stage of mechanization, and our concern here, developed machines to spin cotton into thread. (The second stage developed machines to weave cotton thread into cloth.) The earliest domesticated cottons (ca. 5,000 years ago) apparently grew fibers too short to spin into thread at all, much less by machine. Bolls may have been collected for use as stuffing (e.g., in mattresses). Human selection probably lengthened fiber enough for spinning, first by hand and then by machine. Amerindians and South Asians carried out this selection, and cotton did not grow in England, which throws the invention of spinning machines into a new light. English inventors did not mechanize the cotton industry purely because of their own ingenuity. They used their ingenuity to respond to an opportunity created for them by coevolution between cotton populations and human populations elsewhere. The coevolution began 5,000 years earlier and continued with development of extra-long fiber and adaptation of cotton populations to the West Indies (source of British imports).[35]

A coevolutionary approach helps explain the location and timing of English mechanization in ways that other explanations have not. Historians have credited mechanization to English cultural traits (such as tinkering with machinery, protection of private property, and industriousness) but this hypothesis has a hard time explaining why the breakthrough inventions came at a specific time (the eighteenth century) in a small corner of the island (Lancashire). These cultural traits presumably were common in other parts of the British Isles, too. We can resolve this puzzle if we think of cotton fiber not as a fungible commodity, as economic historians are wont to do, but as the product of populations with different traits. Cotton fiber came from different species in the Old

World and the New World. Old World cottons grew shorter fibers than New World cottons. Length was critical because it affected the strength of thread. Short fibers twisted into weak thread. Long fibers twisted into strong thread. Deft fingers might spin short fibers into (weak) thread adequate for hand weaving, but machines broke short-fibered thread too often to be profitable to spin, much less to weave. So long as England relied on imports of short-fibered cotton from the Old World, it failed to mechanize spinning.[36]

Long-fibered cotton from the New World surged into Lancashire in the 18th century, which partly explains the location and timing of mechanization. Slave ships brought cotton from the New World to Liverpool as part of the triangular trade, and Liverpool supplied surrounding Lancashire. (The port of London imported cotton mainly from the Old World, and the regions surrounding London did not invent the breakthrough spinning machines.) New World cotton cost much more than Old World cotton, but factory owners bought it because they had no choice. In another example of coevolution, the United States became a major supplier only after adapting a population of a Mexican species to grow in upland areas across the South. India, Egypt, and other regions of the world became important industrial suppliers only after they replaced Old World species with populations of New World species that they adapted to local conditions. The textile industry succeeded only because populations of farmers and of cottons continued to coevolve.[37]

This example shows how novel encounters between populations with complementary traits can lead to radical change in history. In this case, the encounter involved a human population in England with certain cultural traits (inventiveness, profit motive, private property, industriousness, etc.) and a cotton population with certain genetic traits (long fiber, among others). Complementarity was a matter of chance. Long fiber coevolved in the Americas and happened to suit the English economic environment. Mechanical inventiveness and other cultural traits evolved in England (among other places) and happened to suit long fibered cotton. Each population's traits were necessary but insufficient for mechanization. If inventiveness were sufficient, England would have mechanized spinning using Old World cottons. If long fiber were sufficient, spinning machines would have originated in the New World. The new combination of a human population with certain cultural traits and cotton populations with certain genetic traits opened an opportunity (not a necessity) to invent machines that helped transform the world.

The story of cotton mechanization highlights the complex, contingent nature of coevolutionary history. It is not reductionist or deterministic, as some historians might fear from an approach that draws on natural science. By stressing culture, it highlights the value of historical topics and methods. By pointing out the importance of non-human populations, it leads to a more complex understanding of causation and consequences than approaches that limit explanations to human actions. By emphasizing variation among and within populations, it highlights the particularity that historians treasure. By examining chance encounters between populations and unconscious selection, it is more contingent than approaches that credit historical change to human intentionality alone.

A construction metaphor helps sum up the significance of coevolution for history (traditionally defined). The fields of human endeavor (economics, politics, etc.) are rooms of a house. The house stands only because it rests on a foundation (agriculture) that has lasted thousands of years. Stones in the foundation are coevolved relationships between populations of people and populations of domestic plants, animals, and microorganisms. When people wanted to expand the house's footprint (migrate elsewhere), they cut more stones (coevolved with new domesticates, and adapted current domesticates to new conditions) to build a wider foundation. As food producers became more efficient, they freed up other people to take up other trades and build the rooms of the house (politicians, religious leaders, artists, and so on). Agriculture created the specialists who built the first story of the house, which has lasted about 12,000 years, as well as the specialists who built the second floor (industrialists) over the past couple centuries or so. The rooms and inhabitants multiplied.

We can extend the metaphor to describe why anthropogenic evolution has been easy to overlook in history. As the house added rooms and stories, inhabitants began to spend more and more time inside their own rooms. Servants delivered food to the rooms, and many inhabitants had never visited the basement, so they had little idea of the house's foundation (coevolution of human and non-human populations). If they ventured out, inhabitants often visited neighboring rooms on the same floor. Political and military leaders, for example, often met for drinks. It became easy to take the foundation for granted and to think that the rooms stood because of what the people inside the rooms did. When inhabitants of rooms wrote reports and memoirs, they described their rooms. If we rely on their records to write history, we stay inside their rooms. If we step outside, it becomes easier to see that historical change is inseparable from changes in populations of non-human species.[38] Coevolutionary history is not disciplinary imperialism by natural science. It is a bridge that enables historians and biologists to coevolve by exchanging ideas that enrich both fields. Historians who cross the bridge will find, in my experience, biologists who welcome our knowledge and approaches.[39]

By capitalizing on the strengths of history and biology, coevolutionary history can prompt new questions and answers. We can start by asking about patterns. Have social divisions among human populations (e.g., along race, class, and gender lines) created differences in traits of populations of other species? Have differences in traits of non-human populations circled back to shape the way human populations have interacted with each other? Have different economic systems shaped populations of a non-human species in different but predictable ways? Have deliberate changes in non-human populations circled back to shape human populations in unintended ways? Have non-human populations developed new traits accidentally that prompted cultural or genetic change in human populations? Have these new traits empowered or disempowered weaker social groups? If we find any of these patterns, we can move on to the two most interesting questions, why and how. Some of the answers are sure to surprise us.

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[1] Massimo Livi-Bacci, *A Concise History of World Population*, 5th ed. (Wiley-Blackwell, 2012), 25.

[2] Edmund Russell, *Evolutionary History: Uniting History and Biology to Understand Life on Earth* (Cambridge University Press, 2011); Edmund Russell, “Evolutionary History: Prospectus for a New Field,” *Environmental History* 8, no. 2 (2003): 204–228; Edmund Russell, “Introduction: The Garden in the Machine: Toward an Evolutionary History of Technology,” in *Industrializing Organisms: Introducing Evolutionary History*, ed. Susan

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R. Schrepfer and Philip Scranton (New York: Routledge, 2004), 1–16. One of several examples of earlier use of evolutionary ideas in history is J. R. McNeill, *Something New Under the Sun: An Environmental History of the Twentieth-Century World* (W. W. Norton & Company, 2001), xxii–xxiv. As research programs, evolutionary and coevolutionary history can contribute to any field that studies interactions among human and non-human populations, such as environmental history, agricultural history, food history, animal history, and medical history. See Donald Worster, “Historians and Nature,” *American Scholar* no. Spring (2010), http://theamericanscholar.org/; Christian W. Simon, “Evolutionary History: Trends in Contemporary History of the Historiography of Environment,” *Storia Della Storiografia* no. 47 (2005): 90–112; Sam White, “From Globalized Pig Breeds to Capitalist Pigs: A Study in Animal Cultures and Evolutionary History,” *Environmental History* 16, no. 1 (2011): 94–120; Christophe Bonneuil and François Hochereau, “Gouverner le « progrès génétique »,” *Annales. Histoire, Sciences Sociales* 63, no. 6 (2008): 1305–1340; Philip Scranton and Susan R. Schrepfer, eds., *Industrializing Organisms: Introducing Evolutionary History* (New York: Routledge, 2004).

[3] Paul R. Ehrlich and Peter H. Raven, “Butterflies and Plants: A Study in Coevolution,” *Evolution* 18 (1964): 586–608; Douglas J. Futuyma and Montgomery Slatkin, *Coevolution* (Sunderland, MA: Sinauer Associates, Inc., 1983). The concept of coevolution has also been used to study the mutual shaping of genes and culture within human populations. See William H. Durham, *Coevolution: Genes, Culture, and Human Diversity* (Stanford, CA: Stanford University Press, 1991).

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[4] Fredrik Backhed et al., “Host-Bacterial Mutualism in the Human Intestine,” *Science* 307 (2005): 1915–1920; Jian Xu et al., “Evolution of Symbiotic Bacteria in the Distal Human Intestine,” *PloS Biology* 5, no. 7 (2007): 1574–1586; Amber Benezra, Joseph DeStefano, and Jeffrey I. Gordon, “Anthropology of Microbes,” *Proceedings of the National Academy of Sciences* 109, no. 17 (2012): 6378–6381; Hachung Chung et al., “Gut Immune Maturation Depends on Colonization with a Host-Specific Microbiota,” *Cell* 149, no. 7 (2012): 1578–1593; Human Microbiome Project Consortium, “Structure, Function and Diversity of the Healthy Human Microbiome,” *Nature* 486, no. 7402 (2012): 207–214; Tanya Yatsunenko et al., “Human Gut Microbiome Viewed Across Age and Geography,” *Nature* 486, no. 7402 (2012): 222–227; Manimozhiyan Arumugam et al., “Enterotypes of the Human Gut Microbiome,” *Nature* 473, no. 7346 (2011): 174–180.

[5] The popular view of evolution described here emerged in individual conversations with scholars, questions at conferences and seminars, and comments by manuscript reviewers.

[6] Eric R. Pianka, *Evolutionary Ecology*, 6th ed. (San Francisco: Addison Wesley Longman, 2000); Brian and Deborah Charlesworth, *Evolution: A Very Short Introduction* (Oxford: Oxford University Press, 2003), 5–6; Douglas J. Futuyma, *Evolutionary Biology*, 3rd ed. (Sunderland, MA: Sinauer Associates, 1998), glossary. For examples of evolution in the wild, see Peter R. Grant, *Ecology and Evolution of Darwin’s Finches* (Princeton: Princeton University Press, 1999); B. Rosemary Grant and Peter R. Grant, *Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galápagos* (Chicago: University of Chicago Press, 1989); for an accessible overview of research on contemporary evolution in Darwin’s finches, see Jonathan

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Weiner, *The Beak of the Finch: A Story of Evolution in Our Time* (New York: Knopf, 1994).

[7] Eve Abe, “Tusklessness Amongst the Queen Elizabeth National Park Elephants, Uganda,” *Pachyderm* 22 (1996): 46–47; H. Jachmann, P. S. M. Berry, and H. Imae, “Tusklessness in African Elephants: A Future Trend,” *African Journal of Ecology* 33 (1995): 230–235; Anna M. Whitehouse, “Tusklessness in Elephant Population of the Addo Elephant National Park, South Africa,” *Journal of the Zoological Society of London* 257 (2002): 249–254.

[8] R. S. Phillips, “Current Status of Malaria and Potential for Control,” *Clinical Microbiology Reviews* 14, no. 1 (2001): 208–226; J. F. Trape, “The Public Health Impact of Chloroquine Resistance in Africa,” *The American Journal of Tropical Medicine and Hygiene* 64, no. 1–2 (2001): 12–17; J. A. Najera, “Malaria Control: Achievements, Problems and Strategies,” *Parassitologia* 43, no. 1–2 (2001): 1–89; Stephen R. Palumbi, *Evolution Explosion: How Humans Cause Rapid Evolutionary Change* (New York: W.W. Norton, 2001), 137–138; Peter B. Bloland, *Drug Resistance in Malaria* ([no city]: World Health Organization, 2001), 2.

[9] Charles Darwin, *Variation of Animals and Plants Under Domestication*, vol. II (Baltimore: Johns Hopkins University Press, 1998), 176–178; Charles Darwin, *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life,* 6th ed. (London: Odhams Press, 1872), 102; Palumbi, *Evolution Explosion*; David W. Ow et al., “Transient and Stable Expression of the Firefly Luciferase Gene in Plant Cells and Transgenic Plants,” *Science* 234 (1986): 856–859; Diane Boyhan and Henry Daniell, “Low-cost Production of Proinsulin in Tobacco and

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Lettuce Chloroplasts for Injectable or Oral Delivery of Functional Insulin and C-peptide," *Plant Biotechnology Journal* 9, no. 5 (2011): 585–598; Erika Sasaki, Hiroshi Suemizu, and Akiko Shimada at al., "Generation of Transgenic Non-human Primates with Germline Transmission," *Nature* 459 (2009): 523–528.

[10] Neus Ferrer-Miralles et al., "Microbial Factories for Recombinant Pharmaceuticals," *Microbial Cell Factories* 8, no. 1 (2009): 17.

[11] Robin W. Winks, *World Civilization: A Brief History*, 2nd Edition (Rowman & Littlefield Publishers, 1993), 20; Steven Wallech et al., *World History: A Concise Thematic Analysis*, ed. Brenda Farrington, vol. 1 (Wiley-Blackwell, 2007), 5; Jared M. Diamond, *Guns, Germs, and Steel: The Fates of Human Societies* (New York: Norton, 1999); Donald Worster, "Transformations of the Earth: Toward an Agroecological Perspective in History," *The Journal of American History* 76, no. 4 (March 1990): 1087–1106; for a challenge to the traditional definition of history, see Daniel Lord Smail, *On Deep History and the Brain* (Berkeley: University of California Press, 2008), 1-73.

[12] For summaries of common views of historians, I looked to textbooks of world history. An example of a description emphasizing human initiation and control of domestication comes from Robin Winks. "The earliest history of agriculture is that of the slow process of finding and selecting suitable wild grains, remaining long enough in one location to cultivate them, [etc.]." Winks, *World Civilization*, 20. Wallech et alia describe something similar for animals: "To domesticate members of any wild species of animal, a human first had to tame the individual animal and then successfully breed it in captivity." Wallech et al., *World History*, 1:15. Some evolutionary biologists emphasize one-way impacts, too. David Mindell says, "Humans created dogs from wolves. Wolves have

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been our partners, but, as with all domestications, we have driven the process." David A. Mindell, *The Evolving World: Evolution in Everyday Life* (Cambridge, Mass.: Harvard University Press, 2006), 56.

[13] Some historians have emphasized the reciprocal nature of obligations created by domestication. Wallech et alia write, "At the heart of domestication is a special relationship between organisms from two different species that requires both to maintain a long and productive association with one another: symbiosis." Wallech et al., *World History*, 1:14. Bruce D. Smith, "Documenting Domesticated Plants in the Archaeological Record," in *Documenting Domestication: New Genetic And Archaeological Paradigms*, ed. Melinda A. Zeder et al. (Berkeley: University of California Press, 2006), 15–24, see 17 (emphasis in original).

[14] Russell, *Evolutionary History*, 57–70; Diamond, *Guns, Germs, and Steel*, 89.

[15] L. N. Trut, "Experimental Studies of Early Canid Domestication," in *The Genetics of the Dog*, ed. A. Ruvinsky and J. Sampson (New York: CABI, 2001), 15–41; A. B. Munkacsi et al., "Convergent Coevolution in the Domestication of Coral Mushrooms by Fungus–growing Ants," *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271, no. 1550 (2004): 1777–1782; Bernhard Stadler and Anthony F.G. Dixon, "Ecology and Evolution of Aphid-Ant Interactions," *Annual Review of Ecology, Evolution, and Systematics* 36, no. 1 (2005): 345–372; Ulrich G. Mueller, Stephen A. Rehner, and Ted R. Schultz, "The Evolution of Agriculture in Ants," *Science* 281, no. 5385 (1998): 2034–2038.

[16] Stephen Budiansky, *The Covenant of the Wild: Why Animals Chose Domestication* (New York: William Morrow, 1992).

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[17] Recent research has suggested a third form of inheritance, epigenetics, in which individuals inherit acquired traits without changing the underlying DNA. Durham, *Coevolution: Genes, Culture, and Human Diversity*; Robert Boyd and Peter J. Richerson, *Not by Genes Alone: How Culture Transformed Human Evolution* (Chicago: University of Chicago Press, 2005); Robert Boyd and Peter J. Richerson, *The Origin and Evolution of Cultures* (New York: Oxford University Press, 2005); Luigi Luca Cavalli-Sforza and Marcus W. Feldman, *Cultural Transmission and Evolution: A Quantitative Approach* (Princeton, NJ: Princeton University Press, 1981); Eric J. Richards, "Inherited Epigenetic Variation--Revisiting Soft Inheritance," *Nature Reviews Genetics* 7 (2006): 395–401. My aim in defining *culture* is to clarify its meaning in this essay, not to suggest that this definition is superior to, or should replace, others.

[18] Diamond, *Guns, Germs, and Steel*, 120.

[19] S. A. Tishkoff et al., "Convergent Adaptation of Human Lactase Persistence in Africa and Europe," *Nature Genetics* 39, no. 1 (2007): 31–40; J. Burger et al., "Absence of the Lactase-Persistence-Associated Allele in Early Neolithic Europeans," *Proceedings of the National Academy of Sciences of the United States of America* 104, no. 10 (2007): 3736–3741; T. Bersaglieri et al., "Genetic Signatures of Strong Recent Positive Selection at the Lactase Gene," *American Journal of Human Genetics* 74, no. 6 (2004): 1111–1120; N. S. Enattah et al., "Independent Introduction of Two Lactase-persistence Alleles into Human Populations Reflects Different History of Adaptation to Milk Culture," *American Journal of Human Genetics* 82, no. 1 (2008): 57–72; F. Imtiaz et al., "The T/G 13915 Variant Upstream of the Lactase Gene (LCT) Is the Founder Allele of Lactase Persistence in an Urban Saudi Population," *Journal of Medical Genetics* 44, no. 10 (2007): e89; S. Myles

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et al., “Genetic Evidence in Support of a Shared Eurasian-North African Dairying Origin,” *Human Genetics* 117, no. 1 (2005): 34–42; N. S. Enattah et al., “Evidence of Still-ongoing Convergence Evolution of the Lactase Persistence T-13910 Alleles in Humans,” *American Journal of Human Genetics* 81, no. 3 (2007): 615–625.

[20] Kevin N. Laland, John Odling-Smee, and Sean Myles, “How Culture Shaped the Human Genome: Bringing Genetics and the Human Sciences Together,” *Nature Reviews Genetics* 11 (2010): 137–148.

[21] J. Rushen, A.M.B. de Passillé, and L. Munksgaard, “Fear of People by Cows and Effects on Milk Yield, Behavior, and Heart Rate at Milking,” *Journal of Dairy Science* 82, no. 4 (April 1999): 720–727.

[22] I do not know whether he “intended” to train me or not; the effect was that I learned to behave a certain way in response to his cue.

[23] Alan L. Olmstead and Paul W. Rhode, “Biological Innovation and Productivity Growth in American Wheat Production, 1800-1940,” *Journal of Economic History* 62 (2002): 581; Alan L. Olmstead and Paul W. Rhode, “Biological Innovation in American Wheat Production: Science, Policy, and Environmental Adaptation,” in *Industrializing Organisms: Introducing Evolutionary History*, ed. Susan R. Schrepfer and Philip Scranton (New York: Routledge, 2004), 43–83.

[24] Alan Olmstead and Paul W. Rhode, *Creating Abundance: Biological Innovation and American Agricultural Development* (New York: Cambridge University Press, 2008).

[25] Smith, “Documenting Domesticated Plants in the Archaeological Record”; Melinda A. Zeder, “Archaeological Approaches to Documenting Animal Domestication,” in

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Documenting Domestication: New Genetic And Archaeological Paradigms, ed. Melinda A. Zeder et al. (Berkeley: University of California Press, 2006), 171–180.

[26] J. O. Ware, “Plant Breeding and the Cotton Industry,” in *Yearbook of Agriculture 1936* (Washington, D.C.: U.S. Government Printing Office, 1936), 657–744.

[27] This section builds on ideas in Edmund Russell et al., “The Nature of Power: Synthesizing the History of Technology and Environmental History,” *Technology and Culture* 52, no. 2 (2011): 246–259; for basic concepts of energy and power, see Vaclav Smil, *Energy in World History* (Boulder: Westview Press, 1994), 1–11. In this essay, I am using *social power* in the instrumental sense of Max Weber when he wrote, “In general, we understand by ‘power’ the chance of a man or of a number of men to realize their own will in a communal action even against the resistance of others who are participating in the action.” Women should be included in this definition. Max Weber, *From Max Weber: Essays in Sociology*, trans. H.H. Gerth and C. Wright Mills (New York: Oxford University Press, 1946), 180. I am defining *social power* to clarify its usage in the essay, not to suggest that this definition is superior to, or should supplant, others (which are numerous).

[28] Smil, *Energy in World History*, 6, 94, 225.

[29] Smil, *Energy in World History*, 6, 39–49.

[30] Smil, *Energy in World History*, 28–91.

[31] Smil, *Energy in World History*, 40–49 ; Brian Donahue, *The Great Meadow: Farmers and the Land in Colonial Concord* (Yale University Press, 2007).

[32] Smil, *Energy in World History*, 92–156.

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[33] Russell, “Introduction: The Garden in the Machine: Toward an Evolutionary History of Technology”; Scranton and Schrepfer, *Industrializing Organisms: Introducing Evolutionary History*.

[34] Thomas Finger is writing a dissertation at the University of Virginia on the importance of American grain for the British Industrial Revolution. His findings, which I draw on here, are summarized in Russell et al., “The Nature of Power: Synthesizing the History of Technology and Environmental History”; Olmstead and Rhode, *Creating Abundance*.

[35] Russell, *Evolutionary History*, 103–131.

[36] Russell, *Evolutionary History*, 103–131.

[37] Russell, *Evolutionary History*, 103–131.

[38] Donald Worster, “Appendix: Doing Environmental History,” in *The Ends of the Earth* (New York: Cambridge University Press, 1988), 289–307.

[39] R. Lee Lyman, “Paleozoology in the Service of Conservation Biology,” *Evolutionary Anthropology: Issues, News, and Reviews* 15, no. 1 (2006): 11–19.