Evolution, consequences and future of plant and animal domestication

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Domestication interests us as the most momentous change in Holocene human history. Why did it operate on so few wild species, in so few geographic areas? Why did people adopt it at all, why did they adopt it when they did, and how did it spread? The answers to these questions determined the remaking of the modern world, as farmers spread at the expense of hunter–gatherers and of other farmers.

Plant and animal domestication is the most important development in the past 13,000 years of human history. It interests all of us, scientists and non-scientists alike, because it provides most of our food today, it was prerequisite to the rise of civilization, and it transformed global demography. Because domestication ultimately yielded agents of conquest (for example, guns, germs and steel) but arose in only a few areas of the world, and in certain of those areas earlier than in others, the peoples who through biogeographic luck first acquired domesticates acquired enormous advantages over other peoples and expanded. As a result of those replacements, about 88% of all humans alive today speak some language belonging to one or another of a mere seven language families confined in the early Holocene to two small areas of Eurasia that happened to become the earliest centres of domestication — the Fertile Crescent and parts of China. Through that head start, the inhabitants of those two areas spread their languages and genes over much of the rest of the world. Those localized origins of domestication ultimately explain why this international journal of science is published in an Indo-European language rather than in Basque, Swahili, Quechua or Pitjantjatjara.

Much of this review is devoted to domestication itself: its origins, the biological changes involved, its surprising restriction to so few species, the restriction of its geographic origins to so few homelands, and its subsequent geographic expansion from those homelands. I then discuss the consequences of domestication for human societies, the origins of human infectious diseases, expansions of agricultural populations, and human evolution. After posing the unresolved questions that I would most like to see answered, I conclude by speculating about possible future domestications of plants and animals, and of ourselves. By a domesticate, I mean a species bred in captivity and thereby modified from its wild ancestors in ways making it more useful to humans who control its reproduction and (in the case of animals) its food supply. Domestication is thus distinct from mere taming of wild-born animals. Hannibal's African war elephants were, and modern Asian work elephants still are, just tamed wild individuals, not individuals of a genetically distinct population born and reared in captivity.

In 1997 I summarized available information about domestication and its consequences for human history in a book[1]. Since then, new details have continued to accumulate, and unanswered questions have come into sharper focus. Sources for statements not specifically referenced will generally be found in refs 1–9.

The past of domestication

Our 'decision' to domesticate

The question "why farm?" strikes most of us modern humans as silly. Of course it is better to grow wheat and cows than to forage for roots and snails. But in reality, that perspective is flawed by hindsight. Food production could not possibly have arisen through a conscious decision, because the world's first farmers had around them no model of farming to observe, hence they could not have known that there was a goal of domestication to strive for, and could not have guessed the consequences that domestication would bring for them. If they had actually foreseen the consequences, they would surely have outlawed the first steps towards domestication, because the archaeological and ethnographic record throughout the world shows that the transition from hunting and gathering to farming eventually resulted in more work, lower adult stature, worse nutritional condition and heavier disease burdens[10,11]. The only peoples who could make a conscious choice about becoming farmers were hunter–gatherers living adjacent to the first farming communities, and they generally disliked what they saw and rejected farming, for the good reasons just mentioned and others.

Instead, the origins of domestication involved unforeseen consequences of two sets of changes — changes in plants and animals, and changes in human behaviour. As initially recognized by Darwin[12], and elaborated by Rindos[13], many of the differences between domestic plants and their wild ancestors evolved as consequences of wild plants being selected, gathered and brought back to camp by hunter–gatherers, while the roots of animal domestication included the ubiquitous tendency of all peoples to try to tame or manage wild animals (including such unlikely candidates as ospreys, hyenas and grizzly bears). Although humans had been manipulating wild plants and animals for a long time, hunter–gatherer behaviour began to change at the end of the Pleistocene because of increasingly unpredictable climate, decreases in big-game species that were hunters' first-choice prey, and increasing human occupation of available habitats[14,15]. To decrease the risk of unpredictable variation in food supply, people broadened their diets (the so-called broad-spectrum revolution) to second- and third-choice foods, which included more small

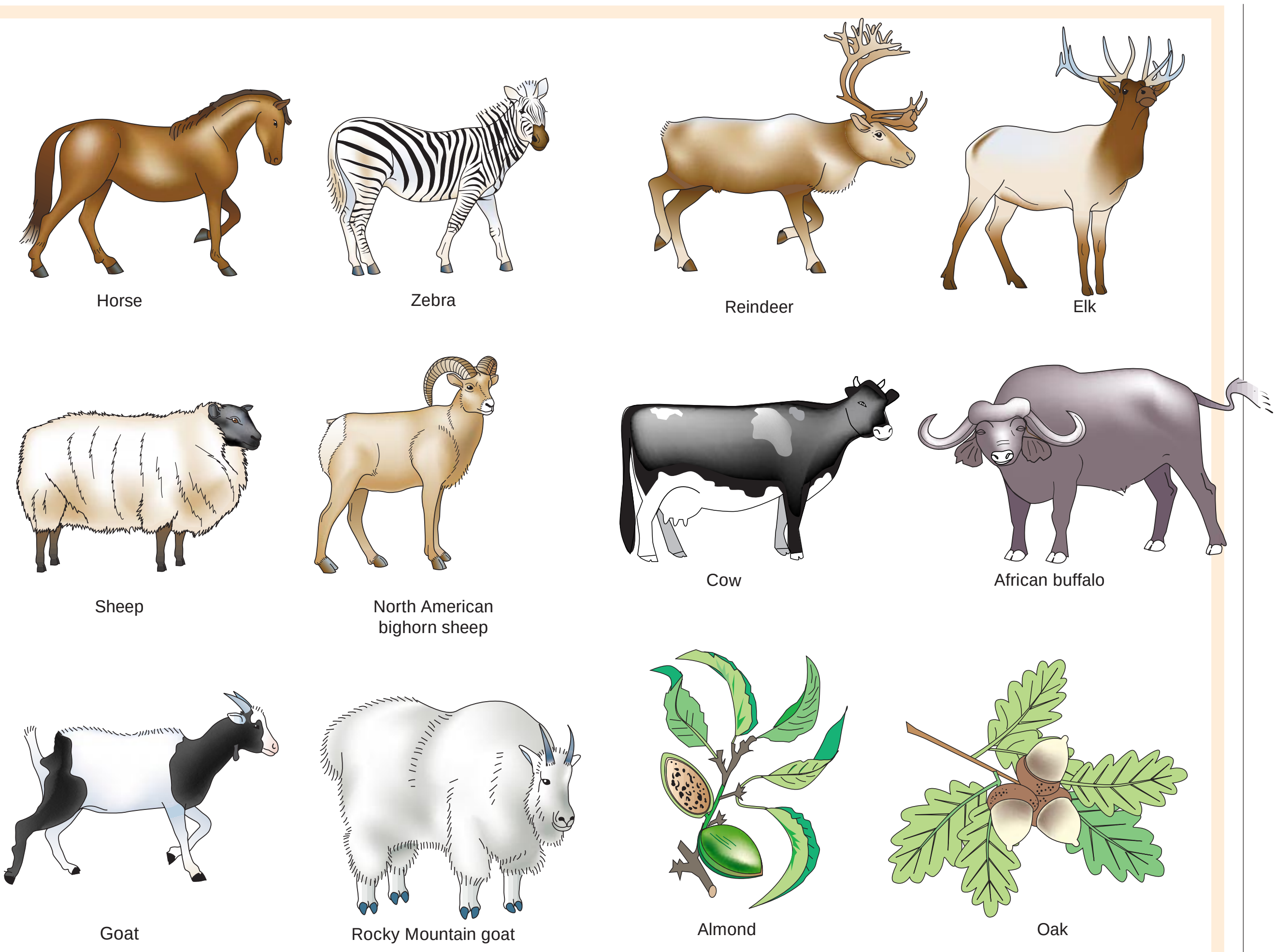

Figure 1 Comparisons of domesticated wild species (left of each pair) and their never-domesticated close relatives (right) reveal the subtle factors that can derail domestication.

game, plus plant foods requiring much preparation, such as grinding, leaching and soaking[14,16]. Eventually, people transported some wild plants (such as wild cereals) from their natural habitats to more productive habitats and began intentional cultivation[17].

The emerging agricultural lifestyle had to compete with the established hunter–gatherer lifestyle. Once domestication began to arise, the changes of plants and animals that followed automatically under domestication, and the competitive advantages that domestication conveyed upon the first farmers (despite their small stature and poor health), made the transition from the hunter–gatherer lifestyle to food production autocatalytic — but the speed of that transition varied considerably among regions[18,19]. Thus, the real question about the origins of agriculture, which I consider below, is: why did food production eventually outcompete the hunter–gatherer lifestyle over almost the whole world, at the particular times and places that it did, but not at earlier times and other places?

Changes of wild species under domestication

These changes are particularly well understood for southwest Asia's Fertile Crescent, the site of domestication that was earliest in the world and that yielded what are still the world's most valuable domestic plant and animal species. For most species domesticated there, the wild ancestor and its wild geographic range have been identified, its relation to the domesticate proven by genetic and chromosomal studies, its changes under domestication delineated (often at the gene level), those changes traced in successive layers of the archaeological record, and the approximate time and place of its domestication identified[9].

For example, wild wheats and barley bear their seeds on top of a stalk that spontaneously shatters, dropping the seeds to the ground where they can germinate (but where they also become difficult for humans to gather). An occasional single-gene mutation that prevents shattering is lethal in the wild (because the seeds fail to drop), but conveniently concentrates the seeds for human gatherers. Once people started harvesting those wild cereal seeds, bringing them back to camp, accidentally spilling some, and eventually planting others, seeds with a non-shattering mutation became unconsciously selected for rather than against[9,17].

Individual wild animals also vary in traits affecting their desirability to humans. Chickens were selected to be larger, wild cattle (aurochs) to be smaller, and sheep to lose their bristly outer hairs (the kemp) and not to shed their soft inner hairs (the wool). Most domestic animals, including even recently domesticated trout[20], have smaller brains and less acute sense organs than do their wild ancestors. Good brains and keen eyes are essential to survival in the wild, but represent a quantitatively important waste of energy in the barnyard, as far as humans are concerned[3,21].

Especially instructive are cases in which the same ancestral species became selected under domestication for alternative purposes, resulting in very different-appearing breeds or crops. For instance, dogs were variously selected to kill wolves, dig out rats, race, be eaten, or be cuddled in our laps. What naive zoologist glancing at wolfhounds, terriers, greyhounds, Mexican hairless dogs and chihuahuas would even guess them to belong to the same species? Similarly, cabbage (*Brassica oleracea*) was variously selected for its leaves (cabbage and kale), stems (kohlrabi), flower shoots (broccoli and cauliflower) and buds (brussels sprouts).

Why so few wild species were domesticated

The wild animal species that most plausibly could have yielded valuable domesticates were large terrestrial mammalian herbivores and omnivores, of which the world holds 148 species weighing 45 kg or more (Table 9.2 of ref. 1). Yet only 14 of those 148 species were actually domesticated (Table 9.1 of ref. 1), prompting us to ask what prevented domestication of the other 134 species? Similarly, worldwide there are about 200,000 wild species of higher plants, of which only about 100 yielded valuable domesticates. Especially surprising are the many cases in which only one of a closely related group of species became domesticated. For example, horses and donkeys were domesticated, but none of the four zebra species congeneric and able to interbreed with them[3,22].

The key question concerning this selectivity of domestication is as follows: in the cases of all those species never domesticated, did the difficulty lie with the species itself, or with the people indigenous to the area to which the species was native? For instance, is the abundance of large wild mammals the reason why no mammal species was ever domesticated in subequatorial Africa, making domestication superfluous for Africans? If that explanation were correct, then African people should also have ignored Eurasian domestic mammals when those were finally introduced to Africa, and European animal breeders on arriving in Africa should have succeeded in domesticating some African wild mammals, but both of those predictions are refuted by the actual course of history.

Six independent lines of evidence[1] converge to prove that, in most cases, the obstacle lay with the species itself, not with the local people: the rapid acceptance of introduced Eurasian domesticates by non-Eurasian peoples; the rapid ancient domestication of the most valuable wild species; the repeated independent domestications of many of them; the failure of even modern European plant and animal breeders to add significantly to our short list of valuable domesticates; ancient discoveries of the value of thousands of species that were regularly harvested in the wild but that never became domesticated; and the identification of the particular reasons preventing the domestication of many of those species.

Comparisons of domesticated wild species with never-domesticated close relatives illustrate the subtle factors that can derail domestication[1] (Fig. 1). For example, it is initially surprising that oak trees, the most important wild food plant in many parts of Eurasia and North America, were never domesticated. Like wild almonds, acorns of most individual wild oaks contain bitter poisons, with occasional non-poisonous mutant trees preferred by human foragers. However, the non-poisonous condition is controlled by a single dominant gene in almonds but polygenically in oaks, so that offspring of the occasional non-poisonous individuals are often non-poisonous in almonds but rarely so in oaks, preventing selection of edible oak varieties to this day. A second example is provided by the European horse breeders who settled in South Africa in the 1600s and — like African herders for previous millennia — tried to domesticate zebras. They gave up after several centuries for two reasons. First, zebras are incurably vicious, have the bad habit of biting a handler and not letting go until the handler is dead, and thereby injure more zoo-keepers each year than do tigers. Second, zebras have better peripheral vision than horses, making them impossible even for professional rodeo cowboys to lasso (they see the rope coming and flick away their head).

Among wild mammal species that were never domesticated, the six main obstacles proved to be a diet not easily supplied by humans (hence no domestic anteaters), slow growth rate and long birth spacing (for example, elephants and gorillas), nasty disposition (grizzly bears and rhinoceroses), reluctance to breed in captivity (pandas and cheetahs), lack of follow-the-leader dominance hierarchies (bighorn sheep and antelope), and tendency to panic in enclosures or when faced with predators (gazelles and deer, except reindeer). Many species passed five of these six tests but were still not domesticated, because they failed a sixth test. Conclusions about non-domesticability from the fact of non-domestication are not circular, because these six obstacles can be assessed independently.

Why there were so few homelands of agriculture

Food production bestowed on farmers enormous demographic, technological, political and military advantages over neighbouring hunter–gatherers. The history of the past 13,000 years consists of tales of hunter–gatherer societies becoming driven out, infected, conquered or exterminated by farming societies in every area of the world suitable for farming. One might therefore have naively anticipated that, in any part of the world, one or more of the local hunter–gatherer societies would have stumbled upon domestication, become farmers, and thereby outcompeted the other local hunter–gatherer societies. In fact, food production arose independently in at most nine areas of the world (Fertile Crescent, China, Mesoamerica, Andes/Amazonia, eastern United States, Sahel, tropical West Africa, Ethiopia and New Guinea).

The puzzle increases when one scrutinizes that list of homelands. One might again naively have expected the areas most productive for farming today to correspond, at least roughly, to the areas most productive in the past. In reality, the list of homelands and the list of breadbaskets of the modern world are almost mutually exclusive (Fig. 2). The latter list includes California, North America's Great Plains, Europe, the pampas of Argentina, the cape of southern Africa, the Indian subcontinent, Java and Australia's wheat belt. Because these areas are evidently so well suited to farming or herding today, why were they not so in the past?

The explanation is that the homelands of agriculture were instead merely those regions to which the most numerous and most valuable domesticable wild plant and animal species were native. Only in those areas were incipient early farmers able to outcompete local hunter–gatherers. Once those locally available wild species had been domesticated and had spread outside the homelands, societies of homelands had no further advantage other than that of a head start, and they were eventually overtaken by societies of more fertile or climatically more favoured areas outside the homelands.

For instance, the Fertile Crescent of southwest Asia was home to wild wheats, barley, peas, sheep, goats, cows and pigs — a list that includes what are still the most valuable crops and livestock of the modern world. Hence hunter–gatherers of the Fertile Crescent domesticated those species and became the world's first farmers and herders, beginning around 8500 BC[1,9,23]. That head start in food production led to them and their close neighbours also developing the world's first metal tools, writing, empires and professional armies. Those tools of conquest, and Fertile Crescent human genes, gradually spread west into Europe and North Africa and east into the western Indian subcontinent and central Asia. However, once those crops, livestock and human inventions had spread, Fertile Crescent societies possessed no other advantages. As all of those elements slowly spread northwest across Europe, farming and power also shifted northwest from the Fertile Crescent to areas where farming had never arisen independently — first to Greece, then to Italy, and finally to northwest Europe. Human societies of the Fertile Crescent inadvertently committed slow ecological suicide in a zone of low rainfall prone to deforestation, soil erosion and salinization.

The spread of food production

From the homelands of domestication, food production spread around the world in either of two ways. The much less common way was for hunter–gatherers outside the homelands to acquire crops or livestock from the homelands, enabling them to settle down as farmers or herders, as attested by archaeological evidence for substantial

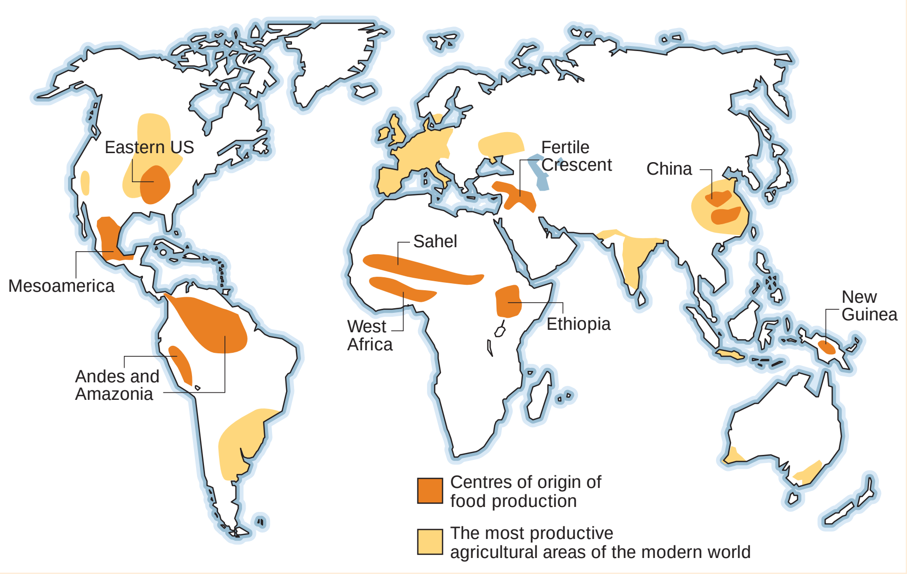

Figure 2 Ancient and modern centres of agriculture. Ancient centres of origin of plant and animal domestication — the nine homelands of food production — are indicated by the orange-shaded areas on the map (based on Fig. 5.1 of ref. 1). The most agriculturally productive areas of the modern world, as judged by cereals and major staples, are indicated by the yellow-shaded areas. Note that there is almost no overlap between the areas highlighted, except that China appears on both distributions, and that the most productive areas of the central United States today approach areas of the eastern United States where domestication originated. The reason why the two distributions are so different is that agriculture arose in areas to which the wild ancestors of the most valuable domesticable crops and animals were native, but other areas proved much more productive when those valuable domesticates reached them.

continuity of material culture, and by genetic, linguistic and skeletal evidence of continuity of human populations. The clearest such example of local adoption of food production is in southern Africa, where around 2,000 years ago some Khoisan hunter–gatherers acquired Eurasian livestock (cattle, sheep and goats) arriving from the north and became herders (so-called Hottentots). Much more often, however, local hunter–gatherers had no opportunity to acquire crops and livestock before they were overrun or replaced by farmers expanding out of the homelands, exploiting their demographic, technological, political and military advantages over the hunter–gatherers.

Expansions of crops, livestock, and even people and technologies tended to occur more rapidly along east–west axes than along north–south axes[1] (Fig. 3). The reason is obvious: locations at the same latitude share identical day-lengths and seasonalities, often share similar climates, habitats and diseases, and hence require less evolutionary change or adaptation of domesticates, technologies and cultures than do locations at different latitudes. Examples include the rapid westwards and eastwards dispersal of wheat, horses, wheels and writing of western Asian origin, and the westwards dispersal of chickens, citrus and peaches of Chinese origin, along the east–west axis of Eurasia. This can be contrasted with the slow spread of Eurasian livestock and non-spread of Eurasian crops southwards along Africa's north–south axis[24], the slow spread of Mexican corn and the non-spread of Mexican writing and wheels and Andean llamas and potatoes along the Americas' north–south axis, and the slow spread of food production southwards along the north–south axis of the Indian subcontinent.

This is not to deny the existence of ecological barriers at the same latitude within Asia and North America, but the general pattern remains. Eurasia's east–west axis, and the resulting rapid enrichment of societies in each part of Eurasia by crops and technologies from other parts of Eurasia, became one of the main ultimate reasons why Eurasian peoples conquered Native American peoples, rather than visa versa. Eurasia's east–west axis also explains why there is much less evidence for multiple independent domestications of the same plant species (see below), and much more evidence for agriculturally driven language expansions, in Eurasia than in the Americas.

Consequences of domestication

Consequences for human societies

Beginning around 8500 BC, the transition from the hunter–gatherer lifestyle to food production enabled people to settle down next to their permanent gardens, orchards and pastures, instead of migrating to follow seasonal shifts in wild food supplies. (Some hunter–gatherer societies in especially productive environments were also sedentary, but most were not). Food production was accompanied by a human population explosion that has continued unabated to this day, resulting from two separate factors. First, the sedentary lifestyle permitted shorter birth intervals. Nomadic hunter–gatherers had previously spaced out birth intervals at four years or more, because a mother shifting camp can carry only one infant or slow toddler. Second, plant and animal species that are edible to humans can be cultivated in much higher density in our gardens, orchards and pastures than in wild habitats.

Food production also led to an explosion of technology, because sedentary living permitted the accumulation of heavy technology (such as forges and printing presses) that nomadic hunter–gatherers could not carry, and because the storable food surpluses resulting from agriculture could be used to feed full-time craftspeople and inventors. By also feeding full-time kings, bureaucrats, nobles and soldiers, those food surpluses led to social stratification, political centralization and standing armies. All of these overwhelming advantages are what enabled farmers eventually to displace hunter–gatherers[1].

Evolution of epidemic infectious diseases

The main killers of humans since the advent of agriculture have been acute, highly infectious, epidemic diseases that are confined to humans and that either kill the victim quickly or, if the victim recovers, immunize him/her for life[1,25–28]. Such diseases could not have existed before the origins of agriculture, because they can sustain themselves only in large dense populations that did not exist before agriculture, hence they are often termed 'crowd diseases'. The mystery of the origins of many of these diseases has been solved by molecular biological studies of recent decades, demonstrating that they evolved from similar epidemic diseases of our herd domestic animals with which we began to come into close contact 10,000 years ago. Thus, the evolution of these diseases depended on two separate roles of domestication: in creating much denser human populations, and in permitting much more frequent transmission of animal diseases from our domesticates than from hunted wild animals. For instance, measles and tuberculosis arose from diseases of cattle, influenza from a disease of pigs and ducks[1]. An outstanding mystery remains the origins of smallpox: did it reach us from camels or from cattle?

Crowd diseases paradoxically became agents of conquest, because exposed individuals acquired immune resistance from childhood exposure, and exposed populations gradually evolved genetic resistance, but unexposed populations had neither type of resistance. In practice, because 13 of our 14 large domestic mammals were Eurasian species, evolution of crowd diseases was concentrated in Eurasia, and the diseases became the most important agents by which Eurasian colonists expanding overseas killed indigenous peoples of the Americas, Australia, Pacific islands and southern Africa.

The agricultural expansions

Because some peoples acquired domesticates before other peoples could, and because domesticates conferred eventual advantages such as guns, germs and steel on the possessors, the history of the past 10,000 years has consisted of farmers replacing hunter–gatherers or less advanced farmers. These agricultural expansions, originating mainly from the nine homelands of agriculture, remade genetic and linguistic maps of the world (Table 18.2 of ref. 1). Among the most discussed (and often highly controversial) possible examples are the expansions of Bantu-speaking farmers out of tropical West Africa over subequatorial Africa[29], Austronesian-speaking farmers out of Taiwan over Island Southeast Asia[30], Fertile Crescent farmers over Europe[31,32], and Korean farmers over Japan[33].

Human genetic evolution

Domestication has been by far the most important cause of changes in human gene frequencies in the past 10,000 years. Among the mechanisms responsible are: the spread of human genes from the agricultural homelands; the evolution of genetic resistance factors (including the ABO blood groups) to our new crowd infectious diseases[34,35]; the evolution of adult-persistent lactase in milk-consuming populations of northern Europe and several parts of Africa; the evolution of allozymes of alcohol metabolism permitting consumption of large quantities of nutritionally important beer in western Eurasia; and the evolution of adaptations to a diet higher in simple carbohydrates, saturated fats and (in modern times) calories and salt, and lower in fibre, complex carbohydrates, calcium and unsaturated fats, than the hunter–gatherer diet[36].

Unsolved questions

Among the host of unsolved questions, I focus here on six: what triggered the emergence of agriculture around 8500 BC and why did it not evolve earlier? Do crop and livestock species stem from a single domestication event or from multiple independent domestications? Can areas of food production be segregated into primary and secondary homelands, the latter describing areas where the arrival of primary homeland crops triggered local domestication? How did food production spread? Why were large domestic mammals predominantly Eurasian? And how can we gain a better understanding of the history of domestication of particular species?

Why then but not earlier?

The human lineage diverged from that of chimpanzees around 6,000,000 years ago. For the next 99.8% of our separate history, there was no agriculture, until it emerged independently in up to nine areas on four continents in the short span of 6,000 years between 8500 and 2500 BC. All of those nearly-simultaneous independent origins seem to be too much of a coincidence. What triggered agriculture repeatedly then, and why had it never arisen during the previous 6,000,000 years?

Posing the question in this way both understates and overstates the puzzle. It understates the puzzle, because there are not only up to nine independent trajectories of intensification that did culminate in agriculture, but also many other ones that didn't quite (or that hadn't yet at the time that European conquest aborted them). Areas of the world where hunter–gatherers in the Holocene developed increased population densities, complex material culture, in some cases pottery, and (some anthropologists argue) sedentary living and ranked societies with chiefs included Mesolithic Europe, Japan and maritime Far East Asia, the North American high Arctic, the Pacific coast of northwest North America, interior California's oak woodlands, the California Channel Islands, the Calusa of Florida, the coast of Ecuador, and the Murray–Darling Basin of southeast Australia (for examples, see refs 37–39). But a similar intensification of hunter–gatherer societies also preceded the emergence of food production in its nine homelands; I suspect that the sole difference between the areas where people remained hunter–gatherers and the areas where food production evolved was that plant and animal species harvested in the latter but not the former areas included ones that automatically evolved domesticates, as already discussed. Thus, there were not just 5–9, but several dozen, independent trajectories of intensification in the Holocene.

On the other hand, my formulation of the question also overstates the puzzle. Only behaviourally modern *Homo sapiens* was biologically and mentally capable of the technological advances and foraging efficiency that resulted in intensified hunting and gathering, and (sometimes) in food production[40]. But behaviourally modern *Homo sapiens* did not emerge until around 55,000–80,000 years ago (the exact date is debated), so we should say that the independent simultaneous emergences were not concentrated in the last 0.2% of hominid history, but 'only' in the last 15% of modern human history. Still, even that seems too concentrated a bout of simultaneous emergences to be coincidental. Was it just that the origins of behaviourally modern *Homo sapiens* set clocks ticking by chance at the same rate all over the globe? That strains credulity, especially as intensified hunter–gatherer economies failed to arise in more areas than the areas in which they did arise.

A possible explanation seems to me to derive from four developments in the Late Pleistocene that may indeed have driven the clock's ticking. First, improvements in human hunting skills and consequent depletion or extermination of large mammalian prey would have made the hunter–gatherer lifestyle less rewarding and less able to compete with food production. Second was the development of human technology to collect, process and store wild foods (such as wild cereals), without which subsequently exploiting the same food species as domesticates would have been impossible (that is, what is the point of sowing wheat if you have not yet determined how to reap, roast and store it?). The third development was the on-going competition between human societies, such that those societies with more effective technology at any moment prevailed over other societies. Fourth, the gradual rise in human population numbers through the Pleistocene required intensified food procurement to feed those larger populations.

Against that background of gradual change, a trigger that may have caused intensification and food production to emerge only after the end of the Pleistocene would have been the end-of-Pleistocene climate changes in temperature, rainfall and unpredictability. These changes could have triggered the broad-spectrum reduction in diet[14–17], and made agriculture possible in areas where it would have been impossible during the Ice Ages (for example, expanding Fertile Crescent woodland habitats with understories of wild cereals[41]). Once food production had thus begun, the autocatalytic nature of the many changes accompanying domestication (for example, more food stimulating population growth that required still more food) made the transition rapid. By this interpretation, the independent emergences of food production are no longer remarkably simultaneous — they could not have happened before the end of the Pleistocene (11000 BC), and after the end of the Pleistocene they occurred at very different times, ranging from about 8500 BC (in the Fertile Crescent) to about 2500 BC (eastern North America). Most of the links in this speculative hypothesis are in obvious need of testing.

Multiple versus single domestications

A long-standing question concerns whether each crop and livestock species stems from a single domestication event within a restricted

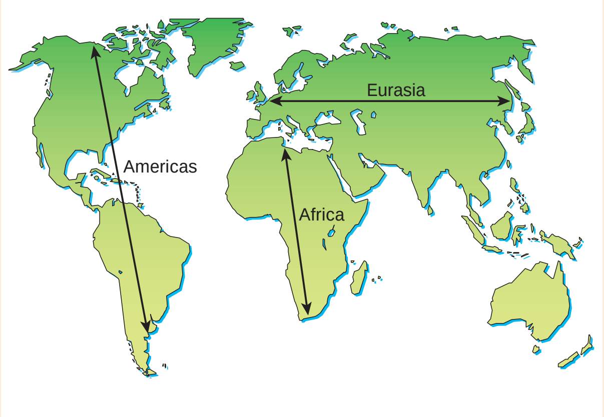

Figure 3 The continental major axis is oriented east–west for Eurasia but north–south for the Americas and Africa. The spread of food production tended to occur more rapidly along east–west axes than along north–south axes, mainly because locations at the same latitudes required less evolutionary change or adaptation of domesticates than did locations at different latitudes. Modified from Fig. 10.1 of ref. 1.

geographic area, or from multiple independent domestications at different sites. An accumulation of recent evidence suggests to me the following generalization: that the former interpretation applies to most major Eurasian crops, the latter interpretation to many New World crops and the major Eurasian livestock species.

Among New World crops, many are represented by distinct but related species in South America, Mesoamerica and the eastern United States, leaving no doubt that related species were domesticated independently in these areas (for example, beans, chenopods, chilli peppers, cotton, squashes, tobaccos and possibly amaranths). Multiple independent domestications are attested within the same species for the chilli pepper species *Capsicum annuum*, common bean *Phaseolus vulgaris*, lima bean *Phaseolus lunatus* and squash species *Cucurbita pepo*[4,7,8,42]. Conversely, the eight crops that founded Fertile Crescent agriculture, with the possible exception of barley, each seem to derive from only a single domestication event[5,9,43–45].

Evidence for separate independent domestications in western and more eastern parts of Eurasia are now available for all of the ‘big five’ domesticated mammals (cow, sheep, goat, pig and horse), plus one of the ‘minor nine’ (water buffalo)[46–54]. For example, cows were domesticated independently in the Fertile Crescent (yielding modern humpless cows), in the Indian subcontinent (yielding modern humped Zebu cows) and in North Africa[46,50,53].

I suggest the following hypothesis to explain predominantly single domestications of Fertile Crescent founder crops, but multiple domestications of Eurasian livestock and many New World crops. Except for barley and flax, the wild ancestors of the Fertile Crescent founder crops had restricted geographic ranges confined to the area between modern Turkey and western Iran, while chickpea was even more narrowly restricted, to southeastern Turkey. Those small geographic ranges, plus the rapid spread of domesticates along Eurasia’s east–west axis, meant that, once a wild plant had been domesticated, it spread so rapidly that further independent domestications of the same or related species were pre-empted. The large Eurasian mammals, however, had such wide geographic ranges (in the case of pigs extending for 13,000 km from Spain to China) that there was ample time for independent domestications at locations west and east of each other. In the New World, even though all the homelands of agriculture lay within only 4000 km of each other, the slowness of crop diffusion along the New World’s north–south axis meant that repeated independent domestications were frequent. So slow was that diffusion that the New World’s main animal domesticates — the llama and guinea pig of the Andes, and the turkey of Mexico — had not even spread the mere 2,000 km north to Mexico and south to the Andes, respectively, by the time that Europeans arrived in AD 1492.

Primary versus secondary homelands

In several parts of the world, food production arose only upon the arrival of domesticates from the primary homelands, whereupon people proceeded to domesticate some local wild plants or animals that had not been domesticated previously[9]. Clear examples of such ‘secondary’ homelands, in which local domestication was triggered by the arrival of Fertile Crescent crops, were Europe (local domestication of poppies and possibly oats) and Egypt (chufa and sycamore fig).

The recognition of those secondary homelands requires us to reconsider the supposed primary homelands. On the one hand, some of the primary homelands may better be viewed as consisting of multiple homelands in which distinct systems of food production arose nearby but independently of each other. This is especially true for the homeland of Andes/Amazonia, which actually comprised primary highland sites in the Andes as well as primary lowland sites scattered from Panama through the Amazon Basin to the Pacific coast of Ecuador and Peru[55,56]. Similarly, the Mesoamerican and Fertile Crescent homelands may have consisted of a mixture of highland and lowland sites, while China probably included northern and southern sites in the Yellow River and Yangtze River basins, respectively, as well as coastal lowland and interior upland sites.

On the other hand, some of the nine candidates for primary homelands may actually be secondary homelands in which domestication was triggered by the arrival of domesticates or of farmers from elsewhere. Independent origins of food production seem indisputable for five of the candidates (the Fertile Crescent, China, Mesoamerica, South America and eastern United States), because they were the earliest sites of domestication in their respective parts of the world. But questions have been raised, at least in conversation, regarding the independence of the other four candidates. Especially uncertain is the status of Ethiopia, where it is unknown whether several undoubted local domesticates (teff, coffee, finger millet, chat, noog and ensete) were cultivated before or only after the arrival of Fertile Crescent domesticates, and the New Guinea highlands, where remains of irrigation and drainage systems attest to early agriculture but where the first crops grown remain unidentified and the earliest dates of food production remain disputed. The independence of even the eastern United States has been challenged recently[42,57], but the evidence seems compelling that Mexican crops arrived there only by way of southwestern United States and only long after local eastern origins of domestication[8,58]. Conversely, in southern India the exact dates of arrival of Fertile Crescent domesticates and of earliest cultivation of local domesticates remain uncertain.

Mechanism of the spread of food production

As already noted, the spread of agriculture from its homelands involved in a few cases the acquisition of domesticates by hunter–gatherers outside the homelands, and in more cases the spread of farmers themselves from the homelands. The contributions of these two processes await resolution in many other cases. For example, contrary to what I wrote five years ago[1], the spread of farming in coastal west Mediterranean Europe (in the form of the Cardial and impressed ware cultures) now seems to have involved the rapid transport by sea of a complete package of Neolithic domesticates around 5400 BC by colonizing pioneer farmers[59]. The Yayoi horizon, which marks the arrival of intensive rice agriculture in Japan, and which Japanese scholars until recently preferred to view as an adoption of mainland practices by the indigenous pre-existing Japanese population, now seems increasingly likely on genetic evidence to represent the arrival, population increase and spread of Korean farmers[33].

Why large domestic mammals were mainly Eurasian

Part of the reason why large domestic mammals were mainly Eurasian is simply that Eurasia, being the largest continent and having escaped the Late-Pleistocene extinctions that eliminated most large mammal species of the Americas and Australia[60], has the largest number of large wild mammal species. But there is a second part to the answer — a much higher percentage of large mammal species proved domesticable in Eurasia (18%) than in any other continent (Table 9.2 of ref. 1). Especially striking is the contrast of Eurasia with sub-Saharan Africa, where none of the 51 large mammal species was domesticable.

This difference constitutes a problem not in human behaviour, but in animal behaviour and sociobiology — something about African environments selected for one or more of the six mammalian traits that made domestication difficult. We already have some clues, as many of Africa's large mammals are species of antelopes and other open-country mammals whose herds lack the follow-the-leader dominance hierarchies characterizing Eurasian cattle, sheep, goats and horses[3,61]. To resolve this problem, I suggest attempting to assign one or more of the six traits derailing domestication to each of the non-domesticated large mammal species of Eurasia and Africa, then evaluating the environmental factors behind the evolution of that trait.

History of domestication of particular species

The history of domestication is much better understood for domesticates of western Eurasia than of other parts of world. Taking Zohary & Hopf's[9] account of western Eurasian plant domestication as a gold standard, it will be a challenge to workers on other biotas to match that standard. Even for western Eurasia, important unanswered questions abound. To mention only one out of dozens, calculation of molecular divergence times between dogs and wolves suggests that domestication of wolves began around 100,000 years ago[62,63], yet the marked morphological differences between wolves and dogs (which should be easily detectable in fossilized skeletons) do not appear until about 11,000 years ago. How can the molecular data and the morphological data be reconciled?

The Future of domestication

Further domestications of plants and animals

We humans today depend for our survival on that tiny fraction of wild species that has been domesticated. Might the rise of molecular biology, genetics and understanding of animal behaviour help feed our growing numbers by increasing that tiny fraction? Modern science has indeed made it technically possible to 'domesticate' species undomesticable in the past, in the sense that we achieve far more draconian control over the captive breeding of endangered California condors (computer-matched for mating to maximize genetic diversity) than the low-tech control that ancient animal breeders exerted over their livestock. But although this 'domestication' is of great interest to conservation biologists, it holds no promise of a condor industry to displace chicken from the supermarkets. What wild species might now be domesticated with profit?

It is instructive to reflect on the meagre additions to our repertoire of domestic species in recent millennia, despite monumental efforts. Of the world's 14 valuable big domestic mammals, the sole addition within the last millennium has been the reindeer, one of the least valuable of the 14. (In contrast, the five most valuable — the sheep, goat, cow, pig and horse — had all been domesticated repeatedly by 4000 BC.) Long-ongoing efforts by modern livestock breeders to domesticate other large wild mammals have resulted either in virtual failure (for example, eland, elk, moose, musk ox and zebra), or else in ranched animals (deer and American bison) that still cannot be herded and that remain of trivial economic value compared to the five most valuable mammals. Instead, all of the mammalian species that have recently become well established as domesticates (for example, arctic fox, chinchilla, hamster, laboratory rat and rabbit) are small mammals dwarfed in usefulness as well as in size by cows and sheep. Similarly, whereas several wild plants were first domesticated only in modern times (for example, blueberries, macadamia nuts, pecans and strawberries), their value is insignificant compared to that of ancient domesticates such as wheat and rice.

Our best hopes for valuable new domesticates lie in recognizing the specific difficulties that previously derailed domestication of particular valuable wild species, and using modern science to overcome those difficulties. For instance, now that we understand the polygenic control of non-bitterness in acorns, perhaps we could use that knowledge to select for oaks with non-bitter acorns, just as ancient farmers selected for non-bitterness controlled by a single gene in almonds. I am concerned, however, that such attempts may in the long run do us more harm than good. Humanity's greatest risk today is of our growing numbers and aspirations ultimately destroying our society by destroying our environment. Providing undernourished people with more food would be a laudable goal if it were inexorably linked to reducing our numbers, but in the past more food has always resulted in more people. Only when crop and animal breeders take the lead in reducing our numbers and our impacts will they end up by doing us net good.

Further domestication of humans

Some genotypes that used to serve us well as hunter–gatherers now serve us poorly as first-world citizens who forage only in supermarkets — especially metabolically thrifty genotypes that now predispose to type II diabetes, salt-conserving genotypes that predispose to hypertension, and other genotypes predisposing to other cardiovascular diseases and lipid disorders. As formerly spartan populations become westernized ('coca-colonized')[64], they fall victim to these diseases of the western lifestyle, extreme examples being the 70% incidence of type II diabetes in those Nauru Islanders and Pima Indians lucky enough to survive to the age of 60 (ref. 65). Because diabetes now afflicts south Asians and Pacific Islanders already in their twenties with high morbidity and mortality, there has been detectable natural selection against the predisposing genotypes even within just recent decades. The lower frequency of type II diabetes in Europeans than in non-Europeans matched for diet and lifestyle suggests that natural selection had already reduced European frequencies of those genotypes in previous centuries, as the western lifestyle was developing in Europe. In effect, the unconscious domestication of humans by agriculture that began over 10,000 years ago is still underway.

Even more such gene-frequency changes, also known as illness and deaths, are expected in the near future, as westernization accelerates in the world's two most populous countries, China and India[66,67]. For example, the incidence of type II diabetes in mainland China, until recently less than 1%, has already tripled in some areas. What lies ahead for China can be projected by considering overseas Chinese populations in Hong Kong, Taiwan, Singapore and Mauritius, where westernization is further advanced and the incidence of type II diabetes is up to 17%. Similarly, the incidence in overseas Indian populations such as that of Fiji gives a foretaste of diabetes' future in India itself.

The resulting projections are that the number of cases of diabetes is expected to increase worldwide by 46% from the year 2000 to 2010, to reach around 220 million in 2010 and around 300 million in 2025. The steepest increase will be in east Asia (including China and India), the projected home of 60% of the world's diabetics in 2010. Similar diet-related disease epidemics are underway in less numerous peoples (from Africans to Aboriginal Australians), involving not just diabetes but also hypertension and other conditions. Thus, these epidemics pose the same dilemma as do efforts to domesticate more wild plant and animal species: how can we ensure that agriculture spreads only happiness, and not suffering as well? ☐

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